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THE NODES OF GRASSES.[1]

MINTIN ASBURY CHRYSLER.

(WITH PLATES I AND II)

ALTHOUGH the stems and leaves of grasses have received a good share of attention from anatomists, and the bundles of the internodes are perhaps sufficiently well known, the nodes have been largely neglected. The reason for this may be the supposed difficulty of unraveling the tangle of bundles found in the node, or the obstacles which the sclerified tissues offer to the preparation of satisfactory sections. Yet the nodes are probably the most interesting regions of the grass stem, for they lack the comparative uniformity of the internodes. Since the application of the celloidin method to hard tissues the difficulties of cutting the necessary serial sections have been removed, so that we are now in a position to know intimately the structure of these critical regions of the stem.

The object of the present account is to trace the course of the bundles of the grass stem, and to discuss the significance of certain structures which make their appearance at the nodes, in particular the amphivasal bundles and cambium. The investigation has been confined to forty-five genera, but since these represent the eleven largest tribes and there is a considerable degree of uniformity in structure, the account is believed to represent the family fairly from the standpoint chosen.

The salient features may best be brought out by the description of types selected to illustrate certain points. The first to be considered represents a medium condition as regards both taxonomic position and ecological relations.

[1] Contributions from the Phanerogamic Laboratories of Harvard University. No. 3.

Avena barbata.—At a short distance above a node the stem presents a simple structure compared with that of many grasses, showing just two circles of collateral bundles surrounding a central cavity. The inner circle of bundles lies at the periphery of the central cylinder, which in this genus is not clearly marked off from the cortex. The bundles of the outer circle lie between groups of cells, which above the leaf-sheath bear chlorophyll; they are considerably smaller than the bundles of the inner ring, and from comparison with corresponding bundles in other genera must be regarded as cortical bundles. In the upper part of a node these assume an amphivasal structure and immediately anastomose with one another and with bundles of the inner circle. But just at this level the structure of the stem is further complicated by the entrance of bundles of the leaf-trace, the course of which must now be described. The leaf-sheath in this species extends a little more than 360° around the stem, and contains, as do most of the genera examined, bundles of two distinct sizes: larger ones, alternating with others which are less than half as great in diameter. These two kinds of leaf-trace bundles have a different course in the stem. The larger bundles undergo a profound modification as they enter the stem, as may be seen by comparing *figs.* 1 and 2, in which the magnification is the same. As such a bundle enters the stem it rapidly increases in size, owing to increase in the number of xylem elements. Most of the added elements are tracheids with more or less suberized scalariform or reticulate thickenings, but some parenchyma cells are also present. These elements gradually extend around the sides of the phloem until this is surrounded by xylem, except a small area on its outer side, which is generally occupied by sclerotic fibres belonging to the group which is so well marked in the sheath (*fig.* 1). In certain species, e. g., *Lolium perenne*, these fibres disappear, and the phloem is completely surrounded by xylem. These bundles evidently must be placed in the amphivasal class. As *fig.* 2 shows, the phloem enlarges very little, but the xylem increases so much that the bundle may be five or six times as broad in the middle of the node as it is in the leaf-sheath. These bundles are by far the most conspicuous objects in a cross-section of the stem at this level. They have a spindle shape which is not due to their oblique course, for they slant

very slightly from the vertical and do not dip deeply into the central cylinder. The xylem consists so largely of tracheids running irregularly and mixed with parenchyma, that the mass has a considerable resemblance to transfusion tissue. Apparently, this region in a bundle forms an important water-storing organ. A further peculiarity of the bundle at this level is the presence of a distinct bundle-sheath or endodermis,[2] consisting of cells whose walls are reticulately thickened and suberized. As these larger leaf-trace bundles descend through the node, branches from the anastomoses mentioned above extend outward between the leaf-trace bundles, and probably anastomose with these, though the fusion is not so plain as in *A. sativa*. Below this level the bundles gradually resume the ordinary collateral shape, lose their endodermis, and run down in a single circle through the internode as already described. The smaller leaf-trace bundles also undergo some expansion as they penetrate to the boundary of the central cylinder, but throughout their course they may be distinguished from the larger bundles, not only by their size but by their early turning outward into the cortex and running down to the next node as the cortical bundles described above.

Though it is not plain in *A. barbata* that the larger leaf-trace bundles are joined, soon after their entrance into the stem, by other bundles of the node, in *A. sativa* and in many other grasses it may clearly be made out that on each flank of the leaf-trace bundle another strand applies itself, swinging through an angle, so that its phloem first joins on, then its xylem. In some species, e. g., *Arundo Donax*, two or more bundles join on each flank of the leaf-trace bundle.

Certain features of the cortical strands are more clearly seen in *Panicularia americana*. The cortical nature of these strands is unquestioned, for they run quite outside the central cylinder, in a wide area of lacunar parenchyma (*fig. 7*). As they reach the upper part of a node they anastomose with one another so as to form a transverse ring or girdle (*fig. 8*), which, at a slightly lower level, sends branches to the bundles of the central cylinder, forming nearly or quite amphivasal bundles, though some of them very soon resume

[2] The term endodermis is here used in the general sense employed by VAN TIEGHEM, rather than in the histological sense proposed by other writers.

the collateral structure which is characteristic of all the bundles of an internode. Further down in the node, the bundles of the leaf-trace enter the central cylinder and the smaller of these anastomose with branches of the nodal complex, and then turn outward to run down through the internode as cortical bundles. The larger leaf-trace bundles behave as in *A. sativa*.

In *Leersia oryzoides* it may plainly be seen from a series of sections, that as each of the smaller leaf-trace bundles enters a node, it is joined by two small bundles from the nodal complex, and this reinforced bundle proceeds downward through the sclerified cortex.

Whether the smaller leaf-trace bundles run down through the cortex, or in the outer region of the central cylinder of an internode, cannot in all cases be determined with certainty, for the boundary of the central cylinder is often poorly marked, and the cortex may be a very narrow zone. Or the boundary of the central cylinder may be marked by a narrow sclerenchymatous ring, and the bundles may lie along this, projecting either towards the inside or the outside. But the position of these bundles inside or outside the central cylinder appears to be a matter of indifference, and in either case they pursue a different course from that of the larger bundles. In a general way it may be stated that the smaller bundles of the leaf-trace, after fusing with bundles from the nodal complex, run downward through the next succeeding internode in the cortex or at its inner border, and at the next node below join with the bundles of the central cylinder. Species to which this statement applies are: *Zizania aquatica*, *Leersia oryzoides*, *Avena barbata*, *A. sativa*, *Panicularia americana*, *P. nervata*, *Agropyron caninum*, *Elymus americanus*, *Triticum sativum*.

The course of the leaf-trace bundles in the grasses, as here described, differs in several respects from the course of such bundles in other families, even in so closely related a family as the sedges, recently described by PLOWMAN (**11**). VAN TIEGHEM'S second class of cortical bundles (**6**, p. 751) corresponds the most closely, and is thus described: "Le faisceau médian de la feuille, qui en prend trois, entre directement dans le cylindre central, tandis que les deux latéraux descendent dans l'écorce pour n'entrer dans le cylindre

qu'au nœud suivant." See further his remarks on the monocotyledons.

Phalaris arundinacea, like Avena, has the bundles of its internode crowded into an annular area surrounding the fistular pith. As these reach the node they anastomose extensively, and at the same time assume the amphivasal condition, which is shown with especial clearness in the variety *variegata*, *figs. 3* and *4*, the latter more highly magnified in order to show the tendency for bundles to form nests of three or more, enclosed by an armor of sclerified fibres. These amphivasal bundles, though abundant in the nodes, are absent from the internodes.

Arundo Donax may be mentioned as typical of species having several circles of bundles surrounding a central cavity. As the leaf-trace bundles enter the stem they swell out, though not to so great an extent as in Avena. The xylem completely encloses the phloem, and the usual suberized sheath of cells with reticulately thickened walls becomes visible. Farther down in the node the leaf-trace bundle is joined on each flank by one or more cauline bundles. The bundles of the latter class are provided with a sheath of heavily thickened cells, and some of them appear to pass through the node without anastomosing with other bundles, though this condition is rare in the members of the family which have fewer bundles. In accordance with the greater thickness of the solid part of the stem, the leaf-trace bundles penetrate more deeply into the central cylinder than in such genera as Avena, making their general course conform more nearly to the palm type of VON MOHL. The number of circles of bundles in an internode appears to be dependent on the size of stem characteristic of the species, and to have little value in establishing relationships.

Grasses with a solid stem conform even more nearly to VON MOHL'S type, for the largest leaf-trace bundles penetrate nearly to the center of the stem, before curving outward and downward toward the periphery of the central cylinder. STRASBURGER (4) has given an excellent account of the course of the bundles in *Zea Mays*. He distinguishes leaf-trace bundles of five different ranks, and finds that the largest of these penetrate most deeply into the stem, while the smallest merely reach the periphery of the central cylinder.

The increase in complexity of the leaf-trace system over the condition found in Avena, seems to be associated with the greater size of the leaf-sheath in Zea; just as a large stem generally has several circles of bundles, so a heavy leaf has a better developed bundle system. Most of the bundles in an aerial node of Zea are collateral, leaving out of consideration the swollen leaf-trace bundles. STRASBURGER (**4**, p. 348) finds amphivasal bundles at the point of origin of axillary buds and adventitious roots; I have confirmed his observation in the former case. Much larger and more numerous amphivasal strands are however to be found in the nodes of the axillary branches bearing the ear of corn. One of these bundles is represented in *fig. 5*. It is only in the leafy part of the branch that these occur, for in the "cob" the bundles are collateral, with an exceedingly well-developed phloem, doubtless associated with the transfer of elaborated food. The amphivasal bundles of these branches are as usual bundle fusions, and their occurrence in the reproductive axis of a plant showing few elsewhere, seems to be a point of some significance, especially when we consider that Zea is probably a highly organized member of the family.

Zizania aquatica merits special attention on account of certain features which may be regarded as primitive, e. g., the six stamens. In an aerial internode a narrow cortex surrounds the hollow central cylinder, and the two are separated by a ring of sclerified cells. Partly imbedded in this ring are a number of small bundles, some of which project into the cortex and on account of their origin must be regarded as cortical bundles. All the bundles are collateral, and those inside the sclerotic ring lie at different depths within the central cylinder. As would be expected from the aquatic habitat of the plant, the xylem is reduced; in fact, in some instances, it is represented only by a cavity, and in all cases it has its vessels very slightly lignified. The phloem does not share in this reduction. As the node is approached the bundles at the periphery of the central cylinder anastomose, at the same time becoming amphivasal, and a number of transverse strands join up some of the inner bundles of the stele with one another. At this level the leaf-trace bundles enter the stem; they are of at least three ranks, and of these the largest penetrate into the central cylinder, enlarging on the way,

owing to increase in the xylem elements, which come to enclose the phloem more or less completely, as already described for Avena. A little further down they are joined on the flanks by several bundles from the internode above, each leaf-trace bundle with its tangle of contributing bundles forming a complex bunch of vascular tissue. A suberized endodermis surrounds the leaf-trace bundles in the node. The second rank of bundles of the leaf-trace also enter the central cylinder, where they are joined by other bundles, but soon return to the periphery of the central cylinder, where they give rise to some of the bundles which run through the next internode below on the border line between the sclerotic ring and the cortex. The smallest bundles of the leaf trace go no deeper than the sclerotic ring, and here fuse with other bundles found in this zone. Thus, the course of the bundles of different rank agrees with what STRASBURGER found in Zea. In the lowest part of the node, the very numerous bundles of the sclerotic ring anastomose and proceed downward, greatly reduced in numbers, while the bundles inside the central cylinder also become much fewer, owing to completion of the fusion of the large leaf-trace bundles with cauline strands.

The basal region of the stem has a cortex which differs from the aerial parts in being much broader and more spongy, on account of the large intercellular spaces. At any of the basal nodes the central cylinder is bounded by an endodermis, consisting of a single layer of rounded cells with suberized walls (*fig. 6*). Inside this is a narrow zone of vascular tissue, whose elements run circularly; then a wide zone, consisting of small bundles running vertically, and so closely packed together that it is generally impossible to distinguish their limits. Bounding the two vascular rings on the inside is a band of sclerified cells which are in contact with the pith. As the photograph shows, leaf-trace bundles make their way into the central cylinder through wide gaps in this four-layered ring, and it may be clearly seen, even in unstained sections, that along the edges of such a gap the external suberized endodermis is continuous with the inner sclerified layer. All of the large leaf-trace bundles pass through such gaps, but the roots leave the central cylinder without causing a gap, as has been observed in plants of various groups. In the pith of the central cylinder are scattered many

bundles, nearly all of which are amphivasal, and where the nodes are crowded, as they are at the very base of the stem, the amphivasal condition is retained by bundles from one node to another, though in the more elongated internodes, found a little higher in the stem, only collateral bundles occur. The contrast between the upper and the basal nodes is indeed striking, for the former show no amphivasal bundles running longitudinally in the pith, except the enlarged leaf-traces. This feature of the aerial node may be partly accounted for by the thinness of the diaphragm in which run the anastomosing bundles, which are generally amphivasal.

AMPHIVASAL BUNDLES

Although these have been repeatedly reported as occurring in the subterranean stems of monocotyledons (see STRASBURGER, **4**, p. 348, footnote; DEBARY, **2**; SCHULZE, **5**)[3], the only references to their occurrence in grasses that have been found are by STRASBURGER (**4**) and JEFFREY (**9**). DUVAL-JOUVE (**1**) figures the rhizomes of many grasses, but shows no amphivasal bundles. Yet an examination of the nodes of some of the same species shows that the bundles in question occur here. Two sorts must be distinguished in this family: (1) the swollen portion of a leaf-trace bundle, the xylem consisting largely of a mass of tracheids running irregularly; (2) the type usually figured, the xylem forming simply a ring of vessels. The features of the first class have been described under Avena. Such a bundle is always enclosed by an endodermis which generally has pitted or reticulated walls, and shows, in addition to the ordinary metaxylem elements, a large number of reticulated tracheids, which almost or quite enclose the phloem. All the species examined show these bundles, from hydrophytes such as Zizania to xerophytes such as Ammophila, and there appears to be no relation between the size which a bundle attains at its widest part and the condition under which the species grows. If, as already suggested, these bundles serve to store up water, it might be expected that they would be poorly developed in aquatics, but the only peculiarity of the bundles found in such plants is the slight lignification of the xylem, a char-

[3] Since the above was written, HOLM has reported the occurrence of amphivasal bundles in the rhizome and also the aerial stem of *Croomia pauciflora* (Amer. Jour. Sci. **20**:50–54. 1905).

acter shared by all the bundles of such plants. Quite commonly, the bundles are surrounded by a layer of parenchyma rich in chlorophyll. This suggests that the node is an active assimilating organ. Bundles of the second class—amphivasal bundles as usually understood—are found in the nodes of the great majority of the grasses examined, but are especially numerous in the following species: *Coix lachryma, Paspalum stoloniferum, Panicum sanguinale, Sorghum halepense, Leersia oryzoides, Phalaris arundinacea, Calamagrostis canadensis, Avena barbata, Panicularia americana, Panicularia nervata, Festuca arundinacea, Triticum sativum.* The fact that they are practically confined to the nodal regions, suggests that they are associated with bundle fusions, and this assumption has been amply borne out by observation. Further, since the bundles which fuse are usually traces of leaves which come off higher up, it appears that the occurrence of such bundles is to be referred to the leaves. The closed mode of venation, prevalent in the monocotyledons, involves that a large number of bundles shall run down parallel to one another through the petiole or sheathing base of the leaf. In the grasses the numerous bundles are accommodated in the leaf-sheath, which frequently encircles the stem for somewhat more than 360°. The large number of bundles cannot at once find room in the vascular ring, which we may believe constitutes the primitive stele in both dicotyledons and monocotyledons, according to results of JEFFREY (**8**), and CHRYSLER (**10**). Hence the leaf-bundles, or some of them, pass into the inside of the central cylinder, and sooner or later join other bundles. It will be readily seen that a bundle lying in the pith has a better chance to orient itself with regard to some other bundle which it may join, than has a bundle which merely fits itself into a gap in a vascular ring (e. g., the leaf-trace of a fern such as Adiantum). Hence it is not surprising to find that before two bundles of a monocotyledon fuse, they swing around, so that phloem fuses with phloem, and the xylem accordingly surrounds the compound bundle. How far beyond the point of fusion of the bundles this amphivasal condition persists, is a feature which varies greatly. In most of the grasses the collateral structure is soon resumed, but the example of Zizania shows that, at the base of the stem where the nodes are crowded, the amphivasal condition

may continue through several internodes. This probably accounts for the prevalence of these bundles in the rhizomes of monocotyledons, where they were first observed. A comparison of the aerial and subterranean nodes of the grasses under study has not yielded results of great significance; most species show no noticeable difference in the number of amphivasal strands in the two cases. But in *Andropogon furcatus*, *A. scoparius*, *Chrysopogon avenaceus*, *Zizania aquatica*, and *Phleum pratense*, the amphivasal strands are distinctly more numerous in the basal nodes. No examples of the opposite condition have been found. QUEVA found in Gloriosa (**7**) that the amphivasal bundles are connected with the origin of a branch. Among the grasses, *Phalaris arundinacea*, *Paspalum stoloniferum*, *Sporobolus Wrightii*, *Coix lachryma*, and *Zea Mays* show these bundles at the point of origin of branches, but in other species only collateral bundles could be discovered at these places. Too much importance should not be attached to the few cases named, in view of the fact that the sedges uniformly show amphivasal bundles associated with leaves and not with branches, as PLOWMAN has shown (**10**). This is one reason for considering the grasses a more specialized group than the sedges; in fact it may be premised that the amphivasal condition originally connected with leaf-traces has in the Gramineae spread to the branches. The occurrence of amphivasal bundles in the leafy reproductive axis of Zea, while they are rare in the main stem, deserves emphasis. While many of the grasses show amphivasal bundles in all the nodes, in this highly developed genus the bundles in question have nearly disappeared from the ordinary nodes, but have persisted in the conservative region named. STRASBURGER proposes (**4**, p. 348) a physiological explanation for the occurrence of these bundles, viz., that the amphivasal structure is favorable for the taking up of reserve materials stored in a rhizome, but this explanation is not in accord with the accepted view that elaborated food is carried not by the xylem, but by the phloem. Examination of serial sections leads to the opinion that the mechanical necessities of bundle fusion rather than considerations of absorption of food have been the determining factor in producing these bundles.

If we accept the view advanced above, that these bundles are to

be associated with the large number of leaf-trace bundles of the monocotyledons, their phylogenetic significance is considerable. The ferns and dicotyledons have a comparatively small number of leaf-trace bundles; amphivasal bundles are absent in the former and rare in the latter group, but are widely distributed in the monocotyledons, which accordingly appear to represent a more recent and highly specialized group. In the most highly organized members of the Gramineae, such as Zea, is shown a tendency to reduce the number of amphivasal strands, but even in such cases they may linger on in the reproductive axis. JEFFREY (9) has called attention to the fact that in highly organized families, such as Iridaceae and Orchidaceae, these bundles disappear even from the reproductive axis.

CAMBIUM.

A feature of the vascular bundles of *Avena barbata*, not so far mentioned, is represented, in *fig. 9*, which shows a bundle from the stem at a distance of about 1^{mm} above one of the upper nodes. That the tissues are immature is shown by the presence of protoplasm and a nucleus in certain of the vessels. The shrunken protophloem is represented by the dark band at the outer edge of the bundle, and the metaphloem as usual has its elements arranged irregularly. Between these elements and the vessels are a number of rows of flattened cells, radially arranged, corresponding well to the cambium of dicotyledons. This feature is not confined to the young stem, as is seen in *fig. 10*, which represents a bundle from above one of the lower nodes of the same plant. A few tangential divisions are to be seen in the leaf-trace bundle shown in *fig. 1*, though cambial activity here is slight. Toward the node and farther up in the internode and sheath, this peculiarity is not shown by the bundles, but at the regions mentioned most of the bundles have a more or less clear indication of cambium.

In the leaf-sheath of *Andropogon argenteum* (*fig. 11*), at a distance of $1–2^{mm}$ above its insertion on the stem the larger bundles show an unmistakable cambial layer. From the small amount of phloem or xylem showing radial arrangement of its elements, it appears that the cambium is functional for only a short time. Sections through the leaf-sheath, cut 5^{mm} above the one shown in the figure, still exhibit a layer of radially arranged cells exterior to the xylem,

but the cells have thicker walls and a rounded outline, indicating that in that region the period of activity of the cells is past. The stem of this plant does not show good examples of cambium, nor do *A. scoparius* or *A. furcatus* show the feature, even in the leaf-sheath.

A further example is shown in *fig. 12*, which represents a bundle from the stem of *Erianthus Ravennae* 1–2^{mm} above the level of insertion of the leaf-sheath. A similar appearance is presented by the bundles of the sheath. The leaf-trace bundles of Zizania frequently show a large amount of their phloem radially arranged, in spite of the fact that dicotyledonous aquatics generally show a marked reduction of their cambium. The examples so far cited include only the more striking instances of cambium found in the family. More or less plain evidences of cambium have also been observed in the following species: (1) In both stem and leaf-sheath; *Coix lachryma, Panicum crus-galli, Avena sterilis, Lolium italicum, L. perenne.* (2) In stem; *Tripsacum dactyloides, Miscanthus sinensis, Pennisetum longistylum, Panicum sanguinale, Leersia oryzoides, Sporobolus Wrightii, Calamagrostis canadensis, Arundo Donax, Avena sativa, Briza maxima, Panicularia americana, Bromus inermis, Triticum sativum.* The occurrence of a cambium in the region just above the nodes in grasses recalls the well-known power which members of this family possess of bending upward at these regions if the stem is by any means laid horizontally. In this connection it is of interest to note that PLOWMAN (**11**) has found only traces of cambium in the sedges, and in line with this, the stems of sedges are unable to right themselves if bent over into a horizontal position. Miss ANDERSSON (**3**) has reported the occurrence of a more or less plain cambial zone in the young plants of representatives of many monocotyledonous families. She calls attention to the similarity between the bundles in the seedling of Lilium and those in Ranunculus. The only grass referred to is Zea, in which the mature bundles often show a radial arrangement of the cells between xylem and phloem, as is illustrated by the well-known figure in SACHS' *Text-book*. From the occurrence of cambium in the tuberous stems of Gloriosa, QUEVA (**7**) has already concluded that the monocotyledons are derived from dicotyledons. In the case of the grasses it would seem that the cambium possessed by the ancestors

has been retained in the regions where it is of use. On the other hand, it may be argued that we have here the first appearance of a feature which in the dicotyledons becomes prevalent. But why should the cambium appear only at the nodes, where it is of use? It may be regarded as almost axiomatic that the need for a structure is not a sufficient cause for its appearance. So it seems more reasonable to read the evidence in the way first suggested, viz., that we have here a relic of a structure which was present in the ancestors of the grasses, but has disappeared from most parts of the plant and from most families of monocotyledons, and is retained above the nodes of grasses in connection with their power of bending at these regions. Thus the evidence favors the derivation of the grasses from ancestors having a cambium.

The stele of the grass stem has evidently departed widely from the primitive protostele or siphonostele. It has been repeatedly shown that reproductive axes are able to retain ancestral characters. An examination of this region in seventeen species of grasses belonging to seven of the tribes has failed to disclose any instances where the stele presents the primitive type described by PLOWMAN (11). This result seems to confirm the opinion derived from other considerations, that the Gramineae represent a more specialized group than the Cyperaceae. These considerations may now be stated categorically:

(1) The grass family has adapted itself to every habitat, from salt marsh to pampas, and shows every gradation in habit from the bamboo downward. The sedges are prevailingly hydrophytes, and few of them attain a considerable size.

(2) The hollow stem characteristic of most grasses has probably been derived from a solid stem such as is present in the sedges and most monocotyledonous families.

(3) Amphivasal bundles are not found in so large a proportion of species nor are they as numerous in an individual in the grasses as in the sedges.

(4) In practically all of the grasses the leaf-trace bundles are of at least two ranks, while the sedges show no such distinction.

(5) The floral axis of the grasses does not present the simple type of stele shown by some sedges.

On the other hand, the open sheath of the grass leaf may be considered to be more primitive than the closed sheath of the sedges. Further, the cambium found in the grasses is here considered to be a primitive feature. But on the whole the Gramineae are to be regarded as a more highly specialized family than the Cyperaceae, though the families are evidently very closely related.

Certain anatomical features of the grasses, such as the distribution of the amphivasal bundles, seem to have an important bearing on the phylogenetic position of the family among monocotyledons, but since the anatomy of the group is as yet very imperfectly known, a discussion of this point would be premature.

SUMMARY AND CONCLUSIONS.

1. The grasses depart considerably from the scheme proposed by VON MOHL for the course of the bundles, chiefly owing to the stem being hollow in most cases. The leaf-trace bundles are of at least two ranks; of these the largest penetrate most deeply as they enter the central cylinder, generally receiving one or more bundles on each flank as they pass downward to the lower part of the node; the smaller leaf-trace bundles do not penetrate deeply into the central cylinder, but after anastomosing with other bundles pass downward either in the cortex or at the inner border of this. At the next node lower, these cortical bundles anastomose with one another, and then with the bundles of the central cylinder which have come from fusions with leaf-trace bundles at the next node above.

2. The leaf-trace bundles, especially the larger ones, undergo a marked change as they enter the stem. This consists in the appearance of a distinct endodermis, and in an increase in the xylem, leading to the formation of a greatly swollen amphivasal bundle. Below the node these bundles resume the collateral type.

3. Amphivasal bundles of the ordinary type, though absent in the aerial internodes, are very commonly found in the nodes, and arise by fusion of collateral bundles which are generally leaf-trace bundles. In some species they are more numerous in the nodes at the base of the plant, and where such nodes are crowded, the bundles may retain the amphivasal condition through successive internodes. The presence of amphivasal bundles in reproductive branches of plants in which these bundles are scarce in ordinary

nodes, points to their being an ancestral feature, which, in highly organized members, has disappeared from most parts of the plant, but is retained in the conservative flowering axis. It appears that the amphivasal bundles so characteristic of monocotyledons, in all probability made their appearance in connection with the entry of numerous leaf-trace bundles into the nodes, but that secondarily, in certain instances, they are found to be related to branching.

4. A well-marked, though generally short-lived, cambium occurs in the bundles just above the node or near the base of the leaf-sheath in certain grasses. This fact is considered to lend support to the view that monocotyledons have been derived from some group possessing a cambium, probably the dicotyledons.

5. The anatomical features of the grasses point to their being a more highly specialized family than the sedges.

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HARVARD UNIVERSITY.

LITERATURE CITED.

NOTE.—Practically nothing bearing immediately on the subject of this research has been found in the older literature, so it is not cited here. References to it may be found in DEBARY (**2**), and the text of KNY's *Wandtafeln*.

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EXPLANATION OF PLATES I AND II.

PLATE I.

FIG. 1. *Avena barbata;* leaf-trace bundle in the leaf-sheath 1^{mm} above its insertion on the stem. ×130.

FIG. 2. Same; swollen and amphivasal condition of a leaf-trace bundle in the middle region of node. ×130.

FIG. 3. *Phalaris arundinacea;* section through upper part of a node; near the outside are the leaf-trace bundles, alternating large and small; just internal to these are the nests of amphivasal bundles. ×30.

FIG. 4. Same; one of the nests of amphivasal bundles more magnified; on three sides are leaf-trace bundles. ×150.

FIG. 5. *Zea Mays;* one of the large amphivasal bundles from a node of a reproductive branch. ×115.

FIG. 6. *Zizania aquatica;* part of stele and cortex in basal region of the stem. Two gaps with their leaf-trace bundles are visible. ×35.

PLATE II.

FIG. 7. *Panicularia americana;* section 1^{mm} above node, showing two cortical bundles. ×45.

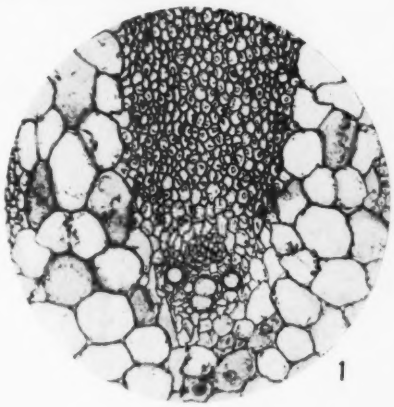
FIG. 8. Same; section from upper part of the node, just above insertion of leaf-sheath. The cortical bundles are connected by a ring-shaped anastomosis. ×45.

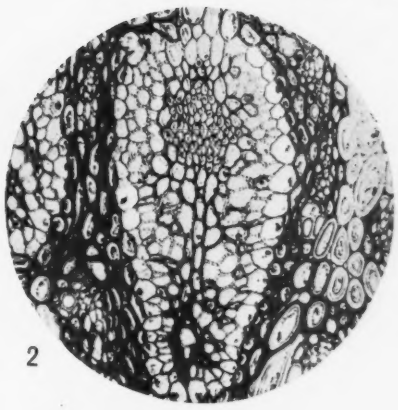
FIG. 9. *Avena barbata;* bundle from a young stem 1^{mm} above insertion of the leaf-sheath, showing cambium. ×150.

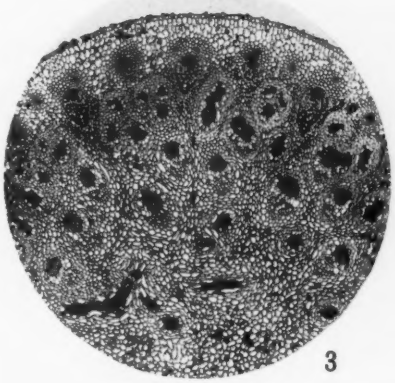
FIG. 10. Same; bundle from the same position in a mature stem. ×150.

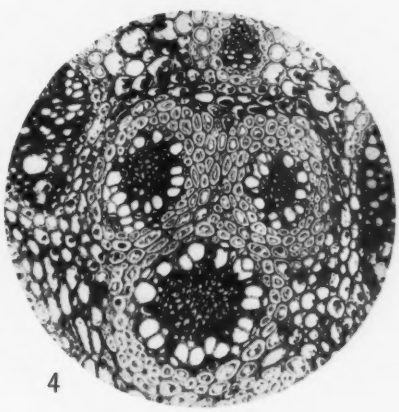
FIG. 11. *Andropogon argenteum;* bundle from the leaf-sheath $1–2^{mm}$ above its insertion on the stem, showing cambium. ×150.

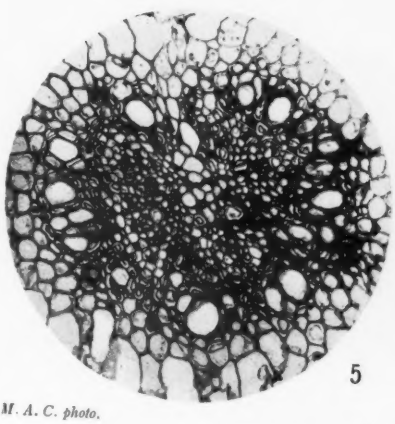
FIG. 12. *Erianthus Ravennae;* bundle from the stem a short distance above a node. ×150.

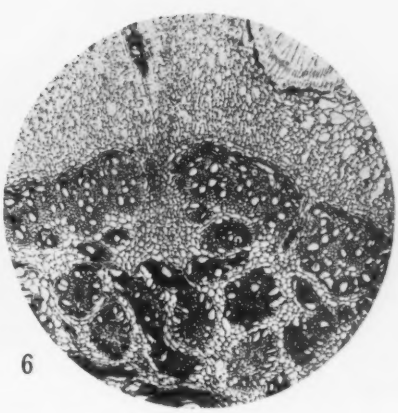












M. A. C. photo.

CHRYSLER on NODES OF GRASSES

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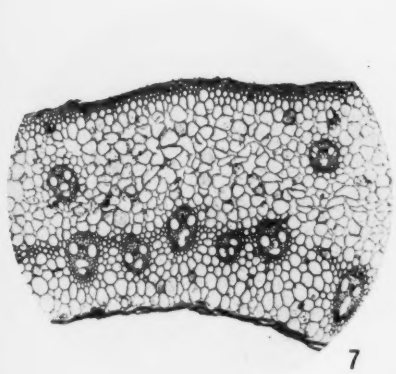

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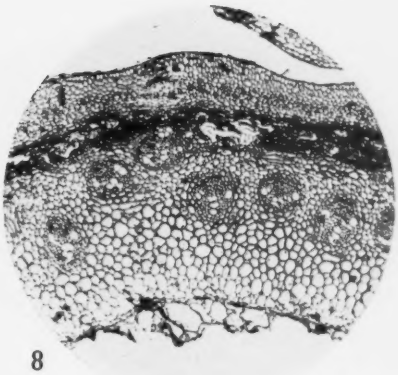

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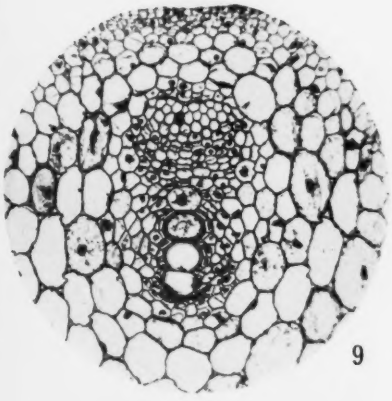

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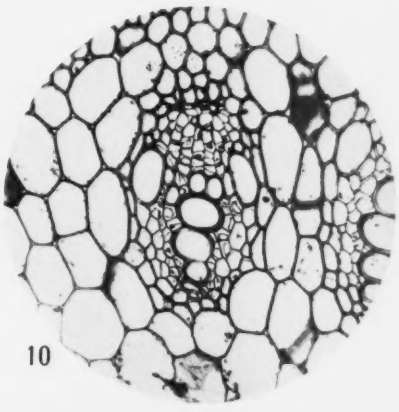

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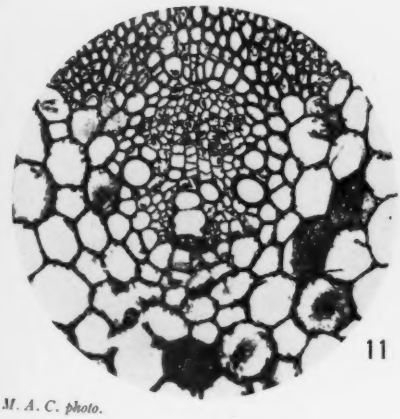

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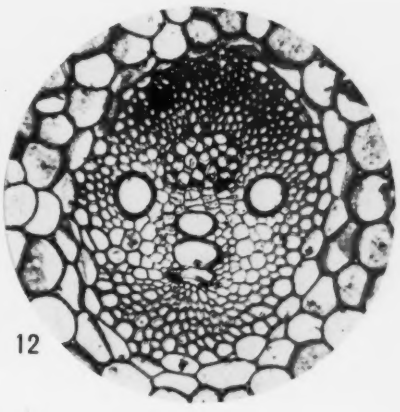

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M. A. C. photo.

CHRYSLER on NODES OF GRASSES

THE BOGS AND BOG FLORA OF THE HURON RIVER VALLEY.

EDGAR NELSON TRANSEAU.

(WITH SIXTEEN FIGURES)

[*Concluded from p. 448.*]

IV. The ecological characteristics of the bog flora and their causes.

The plants occurring in the bog habitat are almost all perennials. In the case of the herbaceous vegetation, the winter is passed by means of subterranean rootstocks. The shrubs are in part evergreen and in part deciduous. The tamaracks and the two birches are deciduous, and the black spruce and pine are evergreen.

Most of the herbaceous and shrubby forms multiply abundantly by vegetative shoots of one form or another. The length of the underground stems of the shrubs is proverbial, but is best appreciated by one who has attempted to dig up one of them entire. In connection with the competition between species for space in the habitat, this is of the greatest importance. A luxuriant growth of cassandra furnishes the most favorable situation for the development of sphagnum in this vicinity. Its profuse branching affords a framework for the upbuilding of the sphagnous layer, its shade properties do not interfere with the photosynthetic work of the moss, and it protects it from the drying effects of wind and direct insolation. Where such associations occur, the difficulties presented for the germination for most seeds, and the efficiency with which competition is combated, are evidenced by the fact that among the tree species only the tamarack, spruce, and pine are successful invaders. All of these plants send out adventitious roots from the stems and branches, and so keep pace with the upward development of the moss. The absence of poplars, willows, red maples, and elms in such *undisturbed* situations must be in part attributed to the completeness with which such territory is controlled by the cassandra-sphagnum association.

ECOLOGICAL ANATOMY.

Aside from the purely aquatic forms which have received much

ecological attention, it is of interest to look at the anatomical characteristics of certain of these plants.

Eriophorum virginicum may be taken as a type of this group, and also of the sedge zone vegetation in general. The culm is very slender and erect, leaves flat, and very narrow, perennial by root stocks. *Stem:* epidermis very thick-walled and cuticularized. As development proceeds, certain radial rows of the primary cortex cells have their walls thickened, and served to connect the tissues of the central cylinder with those of the three or four outer layers of hypodermal cells which also become thick-walled. Between these radial groups of cells lysigenic air cavities are formed. *Root:* epidermal cells in part thin-walled and in part secondarily thickened, no definite arrangement of the thick-walled cells apparent; internal structures closely resemble those of the stem; no mycorhiza present. *Leaf:* outer epidermal cell walls strongly thickened and cuticularized, radial and inner walls less so; lysigenic air spaces traverse the leaf longitudinally; a very thick layer of stereome adjoins the leptome, decreasing to one or two cell layers on the hadrome side of the bundle; chloroplasts massed among the outer layers of the cortex, but occur throughout.

Sarracenia purpurea.—Well known for its insect-capturing pitchers. *Stem:* epidermis and first hypodermal layer thick-walled; lysigenic air cavities throughout pith and cortex; resin deposits confined to the epidermis and one or two hypodermal cell layers, but where wounded heavy deposits of resin take place in the exposed and underlying cells. *Root:* cell walls firm, resinous bodies present throughout, but especially prominent in the two outer cortical layers, in which the cell walls are also strongly thickened. *Leaf:* epidermis thick-walled and slightly cuticularized; stomata on both sides of the lamina, with guard cells strongly cuticularized and slightly protuberant; resinous deposits throughout; inner face of lamina with strong downward pointing bristles.

Oxycoccus macrocarpus.—Stem: pith thick-walled, with resinous bodies; a thick layer of broad-celled bast forms a complete cylinder within the epidermis. *Leaf:* margins revolute, upper epidermis without stomata, heavily cuticularized, radial walls thick, wavy; hypodermal collenchyma of two or three cell layers on leptome side

of midvein, one or two cell layers on the side of the hadrome, development of the stereome cells also smaller on hadrome side; palisade of two cell layers; lower epidermis covered with wax, especially at the stomata, guard cells slightly elevated. Mycorhiza present in the larger roots, wanting in the hairlike branches, no root hairs.

Andromeda polifolia.—Leaf: margins revolute, upper epidermal cells thick-walled, radial walls undulate, no stomata; lower epidermis supplied with unicellular short stiff hairs, and covered with wax, stomata slightly protuberant, strongly cuticularized beneath midvein; palisade of three layers of long narrow cells; stereome strongly developed above and below vascular bundle; on the ventral side this adjoining three layers of large thin-walled air cells and a one-layered hypoderma. *Root:* resinous deposits throughout, no mycorhizal fungi found.

Chamaedaphne calyculata.—Leaf: margin slightly revolute, epidermis thick-walled, heavily cuticularized, cuticle rough, no stomata on upper surface; ventral epidermis covered by shield-shaped multicellular hairs, and a deposit of wax; cuticle unusually thickened beneath the midvein, guard cells sunken, subsidiary cells protuberantr palisade tissue of four or five layers. *Root:* inner and radial walls thickened, cortical tissues thick-walled; resin deposits in vascular bundle and cortex; no mycorhizal fungi found.

Chiogenes hispidula.—Leaf: margin revolute, epidermal walls very thick, cuticle present, papillate, palisade not strongly developed; mesophyll cells in part thick-walled and in part thin-walled; resinous bodies in the epidermis; stomata slightly protuberant. *Stem:* resin present in cortex; mycorhizal fungi in the epidermis of the smaile; roots and throughout the cortex of the larger.

Vaccinium corymbosum.—Leaf: cuticle present, epidermal walls not thickened, palisade of one layer, mesophyll tissues with resinous bodies, cuticle of ventral surface papillate; abundant unicellular hairs on lower epidermis few on upper; leptome side of mid-vein adjoined by three layers of stereome and two or three layers of hypodermal collenchyma, on the hadrome side reduced to two of stereome and two of collenchyma, cuticular papilli usually developed beneath the midvein and at edge of leaf. *Root:* cortical tissue with resin, mycorhiza present. No resin deposits found in stem.

Salix sericea.—Leaf: upper epidermal cells small, strongly cuticularized; mesophyll compact, palisade of two layers of long narrow cells; stomata on under surface, guard cells sunken beneath the slightly protuberant companion cells; hypoderma of five- or six-cell layers on hadrome side, and eight layers on leptome side of midvein. *Root:* resinous bodies present in medullary rays and cortex, the latter consisting of thick-walled cells; no mycorhiza.

Ledum groenlandicum.—Leaf: upper epidermis rugose, with scattered unicellular hairs, margins strongly revolute, cuticle present, cell walls thickened, the radial walls being broadly undulate; lower epidermis covered with a thick cuticle and a felt of long multicellular and short unicellular hairs, glandular hairs usually present near the small veins, stomata protuberant; palisade of three or four layers of broadly oblong cells; beneath vascular tissue of midvein and between the mestome bundles occur large air cells which may form lysigenic air cavities in the older leaves. *Root:* mycorhizal.

Larix laricina.—Leaf: bifacial, deciduous; epidermis thick-walled, slightly cuticularized, guard cells sunken beneath the companion cells; palisade tissue developed toward the dorsal surface, two layers thick showing a radial tendency, stereome reduced to a few cells beneath the leptome; two resin ducts near edges of leaf. *Root:* composed of mycorhiza, resinous deposits throughout, cortical tissues early destroyed by fungus. When grown in culture solutions and well aerated, normal roots with root hairs are produced.

Picea Mariana.—Plants in bogs are stunted. *Leaf:* epidermal cells thick-walled, cuticle present, guard cells sunk beneath the companion cells; mesophyll cells compact, of a more or less radial palisade type. *Root:* mycorhizal, resin deposits throughout, cortical tissues destroyed by fungus. Normal roots are developed under culture conditions.

Pinus Strobus.—Plants very much stunted in the bogs, leaves shorter and thicker. *Leaf,* epidermal walls so greatly thickened that scarcely a lumen remains, beneath this a hypodermal layer of thick-walled cells; mesophyll cells compact and of the usual lobate type. *Root:* mycorhizal, cortical tissues traversed by the fungus hyphae; resinous deposits throughout. *Stem:* annual rings narrow

and distorted, resin bodies throughout cortex and meristematic tissues of the wood.

To summarize these characteristics, it is evident (1) that epidermal and hypodermal tissues are thick-walled; (2) that for the conservation of water these are reinforced outwardly by a heavy cuticle, by coverings of wax and air containing hairs; (3) that resinous bodies are found in the roots and leaves of many of the plants; (4) that there is a general reduction in the size of the leaves, and that these are frequently revolute-margined; (5) that palisade tissue is quite uniformly developed; (6) that mycorhizal fungi are present in the roots of most of the plants; (7) that, when compared with the xerophytes of dry sand plains (**25, 6**), they show a similarity in respect to the reduction in size of the foliage, in the development of external protective coverings of the sub-aerial parts, and in the presence of palisade tissues, but are very different in the matter of root development and character of root structures.

To account for the peculiarities of the bog vegetation various theories have been brought forward. KIHLMAN (**28**), in accounting for the xerophilous character of the plants of arctic swamps, which include several species common to American bogs, lays stress upon two factors: (1) the low temperature of the moist substratum, and (2) the presence of drying winds. The former influences the plants by decreasing the power of absorption, the latter increases the rate of transpiration. The plants of such habitats must therefore be protected against the loss of water by the subaerial parts.

SCHIMPER (**44,** p. 11) in classifying the natural habitats in which xerophytes occur mentions among others "peat bogs, because of the humous acids in the soil." On page 18 he says:

> The xerophilous character of the vegetation of peat moors has hitherto been considered an incomprehensible anomaly, and yet the rich supply of humous acids in the soil furnishes a condition for its occurrence as comprehensible as it is necessary. The presence of Scotch pine and heather on both dry sand and on wet peat is thus not more remarkable than is that of *Ledum palustre*, *Vaccinium uliginosum*, and other peat-plants on the cold dry soil in the polar zones.

Further (p. 124) the statement occurs that "on the very acid humus of moors the vegetation assumes a decidedly xerophilous character, because the humous acids impede the absorption of water by the

roots." However, in describing the arctic vegetation (**44**, pp. 11, 715), he follows the suggestion of KIHLMAN, a conclusion to which he had come independently. GANONG (**16**) also accepts KIHLMAN'S explanation for the xerophilous nature of the raised-bog flora of New Brunswick.

In the study of the structural adaptations of these plants and the causes of their occurrence in bog areas, several questions arise. Are these two factors, cold substratum and acidity, efficient causes of xerophily? Do they act, in the case of the bogs of this region, with sufficient strength to cause xerophilous modifications in the plants there found, or to permit the growth of only such forms as are xerophilous?

The last question may be answered from field observations. They indicate that most low-ground plants grow quite as well on the bog substratum as on the ordinary swamp soils, and that the swamp species of this vicinity may all be found at one place or another growing on bog soils. It would seem that here the bog substratum is no more efficient as a selective agent than are the swamp soils.

The only cases which have come under my observation in southern Michigan which will throw light upon the question of the effectiveness of the temperatures and acidity in the production of xerophilous adaptations is in the case of *Picea Mariana*[7] and *Pinus Strobus*. These two plants both show reduced size of stem and leaf, in the Oxford bog, when compared with plants growing on the margin. But to what extent this may be due to sterility of the bog substratum rather than to temperature and acidity is indeterminable at this time.

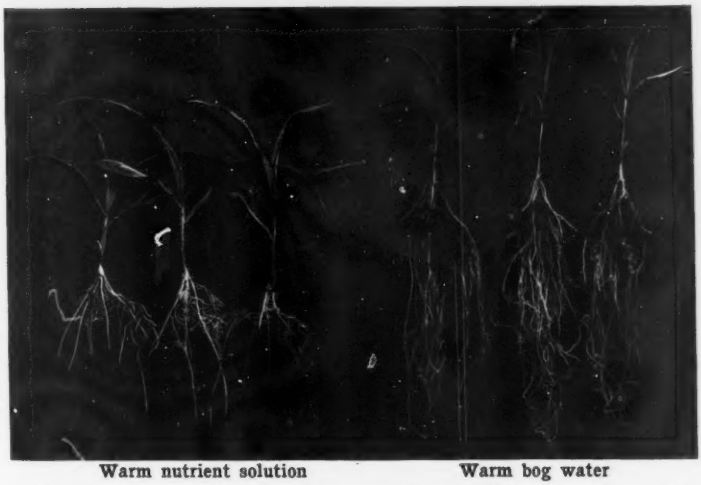
EXPERIMENTS.

To answer the question of the efficiency of a cold substratum and soil acidity to produce xerophily, experiments have been in progress for approximately two years. The difficulties in the way of experimentation along these lines are numerous. The means for controlling soil temperatures in bodies of soil sufficiently large for experimentation with the larger bog plants are practically beyond the possibility of a university laboratory. When it is further realized

[7] The so-called *P. brevifolia* Pk. This form is certainly no more deserving of a distinctive name than is the bog form of the white pine.

that the experiments should extend over a series of years in the case of the shrubby forms, the problem becomes still more complicated.

Cold bog water Cold nutrient solution



Warm nutrient solution Warm bog water

FIG. 12.—Average plants from the several cultures of Indian corn. From photographs.

In order to test the relative effects of humous acids (of the concentration found in the bogs of this vicinity) and low substratum temperatures, experiments were made in the form of water cultures

and with a peat substratum. All of the bog water used was brought to the plant house from the First Sister Lake. The acidity of the water varied from .0005 to .0023 normal acid, as measured by $n/100$ KOH solution.

WATER CULTURES.—(1) The plants were grown in four-liter battery jars covered with a plaster of Paris plate, having five one-inch openings for the passage of the plants and one of smaller size for a thermometer. Four such jars were employed in each experiment, two containing a 0.2 per cent. Knop's solution, and the others bog water. One of each was further maintained at a lower temperature. The cooling was accomplished by passing tap water through 15 feet of quarter-inch ($4.5^{m} \times 7^{mm}$) glass tubing, arranged in a coil within the jar, somewhat below the surface of the liquid. The sides and bottoms of the jars were covered with black paper, and those which were to be cooled were further surrounded by white paper and sphagnum. Daily readings of the temperatures of the air, warm-water solutions and cold-water solutions during the warmest period of the day were recorded. In this way the maximum differences between substrata and air were obtained. As these temperatures were not constant they exaggerate, to a slight degree, the average differences in temperature. Thus, four conditions were obtained which are comparable: (1) warm nutrient solution (temperature approximating that of the air of the plant-house), (2) warm bog solution, (3) cold nutrient solution, and (4) cold bog solution.

Fig. 12 shows the results of one of these experiments with corn. The photograph was taken eighteen days after the experiment was started. When the cultures were set up, the plumule had developed to a length of 2 inches (5^{cm}). The air temperatures during the period of experimentation averaged 18.8° C., that of the warm cultures 18.7° C., and of the cold cultures 10.8° C.

It is to be noted that under these conditions the best growth of the leaves and roots occurred in the bog water. But a reduction of 8° in the substratum temperatures caused a diminution in the development of both leaves and roots; the plants in the nutrient solution and the bog water being equally affected. When all of the plants had developed five leaves, it was noted that in the case of the cold cultures the two lower leaves had withered. This experiment was

repeated with corn, white lupine, and bean under similar conditions, with similar results. The greater development of roots in the case of the warm bog water may be due to the presence of a poison in very minute quantities; but this I have been unable to prove.

(2) A third culture was then made in which five plants of corn were grown in each of the four water culture conditions, and in addition in four similar conditions, using a mixture of sphagnum and peat for the substratum. Wooden boxes 2 feet long, 1 foot wide and a half foot deep ($60\times30\times15^{cm}$) were constructed, and two were lined with galvanized iron. The bottoms of the unlined ones were perforated so as to allow of easy drainage. The lined boxes served for the undrained conditions. Further, in one of the drained and in one of the undrained boxes, 40 feet (12^{m}) of glass tubing, bent into coils, the joints being connected by rubber tubing, were arranged so that a constant flow of cold water, for lowering the temperature, could be maintained. The water level in the undrained bog substratum was kept just below the surface. The water was obtained from the bog at First Sister Lake, but occasionally all were watered with distilled water. The amount added to each box was practically the same. In order to keep the solutions in the water culture jars at the same acidity as in the undrained boxes, the water was siphoned off and transferred once a week. Care was taken in this transfer to aerate the water in the boxes as little as possible, while that of the jars was aerated at irregular intervals by means of a bulb. There were thus produced eight conditions, in which it was possible to test the effect of the acidity of the bog water, of aeration (drainage) of the substratum, and of low temperatures. As a result, it was found that the growth of roots and leaves was best in the warm bog water, in the warm nutrient solution, and in the drained warm peat substratum. Reduction in size of both roots and leaves occurred in the cold bog and nutrient solutions, and in the drained cold and undrained warm and cold peat substrata. But the plants in the undrained cold peat showed the most marked reduction in size. The conclusion was reached (1) that humous acids (acidity varying from .0005 to .0023 normal acid) have no effect upon corn in the matter of leaf and root development; (2) that low temperature and lack of aeration of the substratum both cause reduction in size;

and (3) that when low temperature is combined with poor aeration the effect is very marked.

This experiment was repeated with peas, and the same result was obtained, although the effects were not so marked (*fig. 13*). The roots in the undrained substrata were killed when they attained a depth of a half inch (12^{mm}) below the surface.

(3) In order to test the effects of drainage and of low temperature on bog species, another set of cultures in peat-sphagnum substrata was made. The apparatus used consisted of two flower-pots and two glass dishes aproximately a foot in diameter and three inches

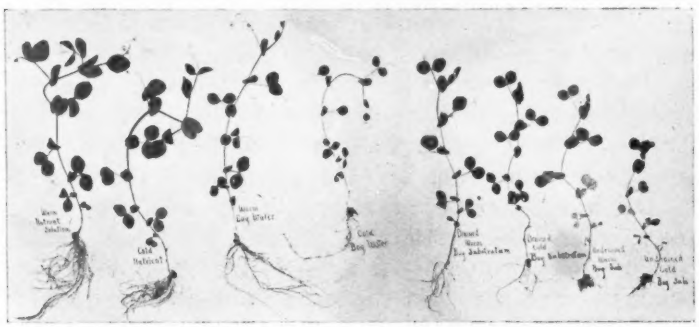
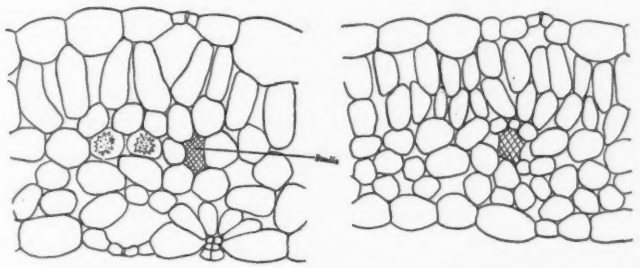


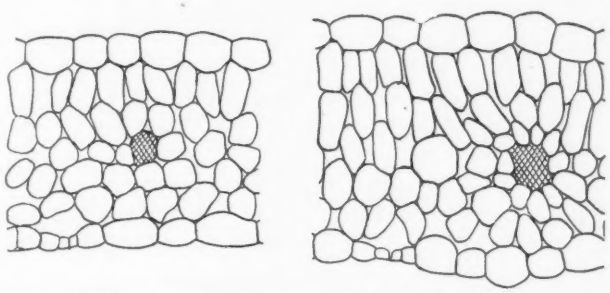
FIG. 13.—Effect of the several conditions upon the development of pea seedlings. All are average specimens. From photographs.

deep (30×7.5^{cm}). A flower-pot and a glass dish were kept cool by passing cold water through fifteen feet of glass tubing arranged in coils, as in previous experiments. Three species were tested in these conditions: two-year-old Larix laricina, *Rumex acetosella*, and *Prunella vulgaris*. The first cultures were made in the spring of 1903 with the Rumex and Prunella. The air temperature averaged about eighteen degrees. The cold substratum was maintained about ten degrees lower. In the case of Rumex it was found that the largest leaves were produced in the drained peat-sphagnum substratum. Lack of drainage and low temperature both caused a reduction in leaf area, and when combined produced leaves which were less than half as large as those of the drained warm substratum.

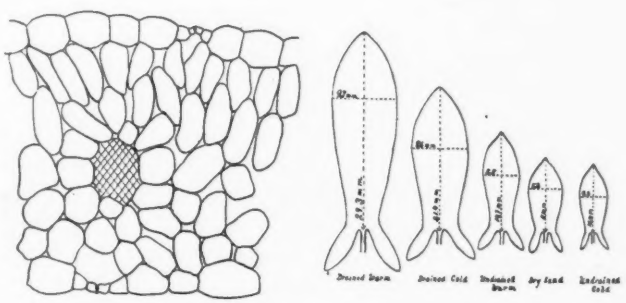
The Prunella under the same conditions showed the same results.



A. Drained warm bog substratum B. Drained cold bog substratum



C. Undrained warm bog substratum D. Undrained cold bog substratum



E. Dry sand F.

FIG. 14.—*A*, *B*, *C*, *D*, *E*, camera drawings of leaf sections resulting from cultures in the five conditions named. ×135. *F*, diagrams showing average length and breadth of leaves.

Fifteen plants were grown in each condition. At the end of the experiment each had produced six to eight mature leaves. The leaves were measured as to length and breadth. An index was obtained by multiplying these two numbers together and averaging for each culture. Following are the indexes of leaf area thus derived: drained warm substratum 1268.3, drained cold 682.6, undrained warm 518.5, undrained cold 421.8.

In the spring of 1904 the experiment with Rumex was repeated. The results correspond with those of the preceding year. The structure of the leaves, resulting in the several cultures, was investigated, and found to show marked variations (**56**). *Fig. 14* represents the cross-sections and average leaf areas produced (seventy-five leaves being measured in each case). When grown on a warm drained substratum, the leaves are large, and the cells are exceedingly loose and turgid. The epidermis is composed of large thin-walled cells, having a thin cuticle outside. The mesophyll consists of a single layer of palisade and three layers of spongy tissue. No resin bodies are present. The plants grown in the undrained substratum, whose temperature was reduced about 8° C. below that of the air, show marked xerophilous characters. The leaf is reduced in area, increased in relative thickness, and the margins become revolute; the epidermal cells are smaller and outwardly thick-walled; a well-marked cuticle is present; the mesophyll is very compact and made up of two or three layers of well-developed palisade cells and three layers of spongy tissue; and in the epidermal cells and those adjacent to the bundles there are marked accumulations of resinous bodies.

For the purpose of comparison, a corresponding set of plants were grown on sand kept just sufficiently moist to allow the plants to live. As will be seen in *fig. 14*, the xerophily is not more marked than that of the undrained cold bog substratum. *Fig. 15* shows the relative appearance of the plants produced by the different conditions.

In the case of the plants grown in the undrained warm and the drained cold substrata, these same effects were noticeable, but to a less marked degree. That, in the case of the undrained cultures, these effects are not due to the acidity of the bog water is shown by

the fact that plants grown in bog-water cultures develop normally.

The light conditions in the several cultures were the same, direct sunlight being avoided by a cloth screen. It is evident that in this case there is no response to strong light in the development of the palisade tissue (**49**). It would seem rather to be a response called forth by a reduced transpiration current (**44**, p. 7). As to function, it may aid in the transfer of food materials as suggested by HABERLANDT (**20**, p. 260).

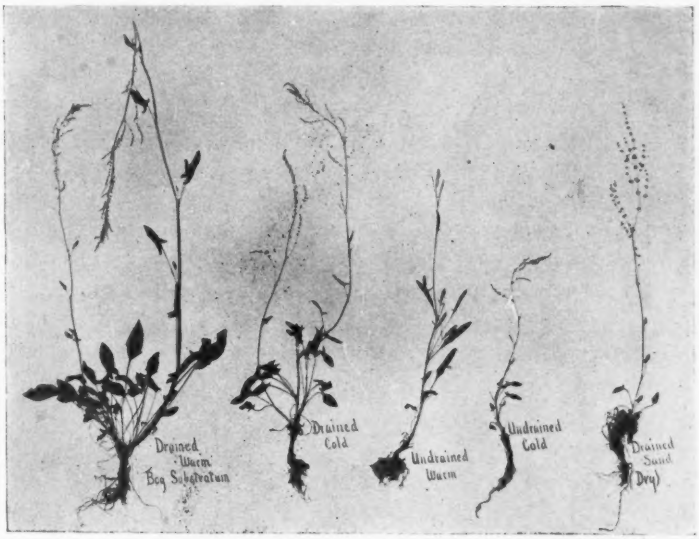


FIG. 15.—Average plants showing effect of surrounding conditions. From photographs.

This plant proved to be the most plastic of all of the species used in the experimentation, and was the only one which showed marked variation in the internal structures. Ecologically the results indicate (1) that an undrained peat substratum may cause xerophilous structures, but that the effect is to be correlated with lack of aeration of the substratum rather than with the acidity; (2) that the same effect may be induced by lowering the substratum temperature (the air temperature remaining the same), and thus impeding the rate of

root growth and absorption; (3) that a cold undrained bog substratum is analogous to a dry warm soil in that both produce physiological drought; (4) that resin bodies, which are characteristic of the bog plants, may be produced by this environment in a plant which under favorable conditions is without them.

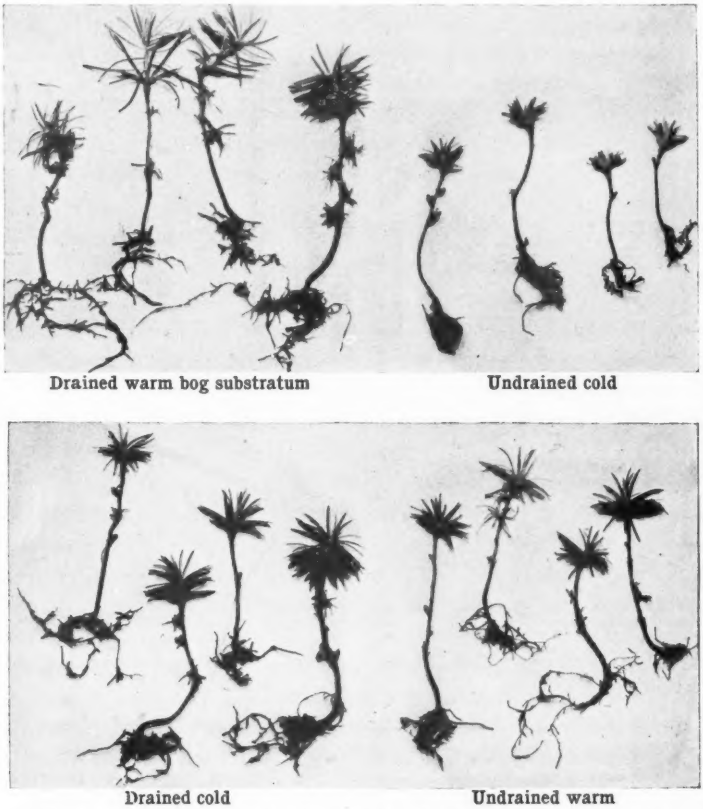


FIG. 16.—Relative effects of drainage and reduced substratum temperature, on Larix. From photographs.

The seedling tamaracks, ten of which were cultivated in each of the four conditions just described for the Rumex, also showed considerable variation. Their relative development at the end of forty-

four days is shown in *fig. 16*. The leaves of the drained warm substratum have an average length of 12.6 mm, of the drained cold 10 mm, of the undrained warm 11.4 mm, and of the undrained cold 6.3 mm. Internally, the leaves show a reduction in the intercellular spaces and in the size of the cells in the case of the plants grown on the undrained cold substratum, when compared with those of the warm drained condition.

(4) In another series of experiments with plants of Larix four to five years old practically the same results were obtained. There were the greatest number and length of leaves and branches produced in the case of the drained warm substratum. The smallest and shortest leaves and branches were produced by the undrained cold substratum.

Experiments with *Ledum Groenlandicum*, *Chamaedaphne calyculata*, *Andromeda Polifolia*, *Betula pumila*, and *Oxycoccus macrocarpus* have failed to produce satisfactory results. This is believed to be due to the shortness of the time under which they were under cultivation. The plants were brought from the bogs in the late autumn and placed in cold frames over the winter. About the beginning of March they were brought into the greenhouse, and after a few days planted in the warm and cold, drained and undrained boxes, previously described. They have grown vigorously, but the differences noticeable may not be correlated with the four conditions. The cranberry has shown the greatest amount of plasticity, but this could not in all cases be correlated with the environment. If these plants can be kept under known conditions for two or more years, it is probable that they will yield valuable results.

(5) In order to test the effect of mineral soils, and the ability to withstand the presence of large quantities of calcium and magnesium, specimens of andromeda, cassandra, and cranberry were grown in sandy loam and sand. They were watered daily with tap water. The cultures were started in the autumn of 1902, and produced vigorous vegetative shoots during the summer of 1903. They failed to bloom, however, and although they are growing well at this time (June 1904), they have again failed to bloom. This may be in part due to the warm plant-house conditions. The experiment was originally started to observe the changes in the roots, and in so far

have been of value. In a sphagnum substratum all three of the plants produced hairlike roots which attain a length of 5–7 cm. The roots are commonly several times branched, very little difference in thickness being shown by the several branches. When grown in sand the roots are still slender, but the frequency of branching is enormously increased. Usually the branching occurs just back of the growing tip. The older root ceases growth as the lateral root develops. The branch continues for 2–3 mm, and it also stops growth with the formation of a second lateral root. The result of this process is a zigzag root showing root branches which have been successively the main root tip. Occasionally several lateral roots develop and the main axis is divided.

(6) The statement that waters containing lime and other mineral salts are unfavorable to the growth of sphagnum has gained wide circulation in ecological literature. Because of the great abundance of lime and magnesia in the waters of this vicinity, I was led to test this fact by growing the sphagnum in tap water and solutions of $CaCO_3$. In one experiment the water in a battery jar was saturated with CO_2, $CaCO_3$ was added in excess, and the CO_2 was again allowed to pass through the water for thirty minutes. In this solution sphagnum was placed, and it has been growing vigorously for three months, although watered daily with water containing over 100 parts of $CaCO_3$ to the million. Some of the sphagnum cultures have been running for ten months, and show no signs of deterioration. Whether the sphagnum of this vicinity has become accustomed to the presence of lime, owing to the nature of the soil waters, or whether sphagnum is generally able to withstand such conditions, remains to be proved. Since the above experiments were performed, I have found an account of somewhat similar experiments by WEBER (**58**), the results of which are the same. It would seem, therefore, that the presence or absence of sphagnum is not to be correlated with the presence or absence of lime.

(7) Among the plants growing in the bogs of this vicinity the following have been found to possess mycorhiza: *Larix laricina, Pinus Strobus, Picea Mariana, Betula lutea, Betula pumila, Oxycoccus macrocarpus, O. Oxycoccus, Chiogenes hispidula, Vaccinium corymbosum, Ledum Groenlandicum, Populus tremuloides.*

In order to get at the conditions which favor or cause the development of mycorhiza, cultures of Larix were made in loose sphagnum, sand, undrained sphagnum, etc. The roots in the many other cultures previously noted were also carefully watched. It has been found without exception that where the plants were grown under properly aerated soil conditions, normal roots developed in place of the mycorhiza. That the acidity of the bog water has nothing to do with the production of mycorhiza is shown by the fact that in water cultures of the same acidity as the solution in the undrained peat, the plants develop normal roots. In the case of roots developed in loose sphagnum, sand, and moist air, an abundance of root hairs were produced. The normal roots in Larix have a diameter about three times that of the mycorhiza, so that when they begin to develop they appear like white pendants from the dark brown mycorhiza. That mychoriza will not develop in a well-aerated substratum was further tested by the following experiment: Two 30^{cm} test tubes were set upright, and 8^{cm} of glass beads were poured into the bottom of each. Into one a glass tube, at whose end were several small openings, was passed to the bottom. The upper part of the tube was connected with a gasometer. Upon this foundation of beads, three plants of Larix were planted in a 5^{cm} layer of peat in each tube. The water level in the two tubes was kept just at the surface, bog water being used throughout. Air was then forced from the gasometer to the bottom of the one tube and allowed to pass slowly through the beads and peat. When the experiment was started, all of the plants possessed only mycorhiza. In the course of a week the aerated plants began to develop normal roots. The experiment was continued for six weeks. The unaerated plants developed only mycorhiza, while those which were aerated developed normal roots.[8] The growth of mycorhiza is exceedingly slow, and the fungus grows with the root. The development of the above ground parts corresponds to the root development. The plants which produce normal roots have longer shoots, and longer, thicker leaves.

It seems evident, in the case of Larix at least, that (1) the mycorhizas develop only in poorly aerated substrata; (2) their growth is

[8] In the case of a number of the plants of Larix grown in the undrained peat in previous experiments, one or two normal roots were developed just at the surface of the substratum.

exceedingly slow, the fungus developing along with the root; (3) the acidity of the substratum is not a factor in their development; (4) in a naturally well-aerated soil or in an artifically aerated substratum normal roots develop; (5) when the roots are not surrounded by water, root hairs develop abundantly. Mycorhiza therefore appears to be an abnormal root condition. Whether the fungus is of advantage to the root under these poorly aerated conditions cannot as yet be stated.

(8) In order to determine whether the zone of tamaracks follows the shrub zone because of the occasional submergence of the sedge zone, the following test was made: Ten Larix seedlings averaging 7^{cm} in height were placed in a crystallizing dish with the roots imbedded in 2^{cm} of sphagnum. Over this a layer of bog water 4^{cm} in depth was maintained for six weeks. The plants grew quite as well as those in a peat substratum. Stem and root submergence is therefore not a factor in preventing the growth of seedlings tamarack in the sedge zone. The liability to submergence in the bogs I have studied would not extend over nearly so long a period of time.

V. Summary.

The Huron River basin shows three well-marked physiographic divisions which differ in forest covering and the possibilities for bog development. These are (1) the region of the Saginaw-Erie interlobate moraine; (2) the Erie morainic belt; and (3) the lake plain.

In discussing the meteorological conditions of a region as affecting the flora, attention is called to the fact that the significance of the data is not apparent unless the temperature and rainfall phenomena are compared with those of the optimum region of dispersal of the plant societies involved. In the case of the bog plant societies the temperature of the region under discussion averages several degrees higher during the summer months than the eastern maritime provinces of Canada (the optimum region of dispersal for the bog plants), while the rainfall during the same period averages about three-fourths as much. This is believed to account for the general difference in character and development of bog societies in the two regions.

Bog and lake basins are here associated with deposits of glacial drift. The most frequent causes of these basins are (1) the melt-

ing of stagnant bodies of ice in old glacial drainage channels after their abandonment; (2) the differential settling of fluvio-glacial deposits; and (3) unequal deposition of glacial material in moraines and till plains.

Marl and peat deposits are commonly associated. The former are of interest in so far as they aid in the filling of the lake basins. Both are formed through plant agencies.

Peat deposits may be classified under two general heads: (1) those connected with glaciation, and (2) those associated with coastal plain phenomena. In North America the bulk of the deposits come under the first head. Their geographic distribution approximates that of the Pleistocene glaciers. Near the southern border the peat areas are scattered, but they become more nearly continuous and more independent of depressions as we go northward. The same effect is brought about in mountainous regions by increased altitude. In the tundra, peat accumulates because of the low temperature and in spite of the scant vegetation. In temperate regions a vigorous vegetation and areas of stagnant water render peat accumulation possible. In the southern coastal plain swamps, peat is formed in stagnant water because of the luxuriant vegetation and in spite of the high temperature.

During peat formation two processes are involved: (1) eremacausis and (2) putrefaction. The former is essentially an oxidizing process, brought about in the presence of air by certain fungi and bacteria. Its products are of direct value as food materials for plants. Putrefaction is carried on in the absence of oxygen and is essentially reduction; the organisms involved are anaerobic bacteria, and the products are of no value to the higher plants as food materials. The accumulation of peat depends upon the scarcity of oxygen below the water level, the acidity of the ground water, and the occurrence of low temperatures.

Peat varies in color beneath the various plant societies, being light brown in the youngest (bog sedge) and dark brown in the oldest, the darkest and most thoroughly decayed form being known as "muck." As disintregration proceeds it brings about a decrease in water capacity, a decrease in volatile combustible matter, and an increase in the amount of ash.

The bog as a habitat for plants differs widely from the other plant habitats of the region in that its substratum has been built by forerunners of the present vegetation. Owing to the influence of the wind in the production of waves, the bogs are largely wanting on the eastern shores of lakes, and in the case of basins which have been almost completely filled with peat, the open water lies toward the eastern margin.

It is well known that bog areas are more liable to late spring frosts than adjoining uplands. This is due to the topography as it affects air drainage, and to the low conductivity of the substratum covering. Under natural conditions it has been found that the areas of cassandra and tamarack dominance are more exposed to late frosts than other societies.

Observations in bog areas show that the soil temperatures beneath the several plant societies differ markedly in range. The records indicate that the areas of bog sedges have temperatures corresponding closely with those of the upland and approximating those of the atmosphere. The willow-sedge (swamp) and maple-poplar areas have slightly lower temperatures during early spring. When the trees leaf out, however, the shade produced causes the maple-poplar area to have the lowest temperatures recorded. The bog shrub and tamarack societies show the lowest average temperature throughout the spring months.

Low soil temperatures retard chemical action, diffusion, solution, and osmosis, and render the substratum unsuited to soil bacteria. When coincident with higher air temperatures, plants having a low transpiration ratio are favored in the competition between species.

In so far as southern Michigan is concerned, the substratum temperatures prevailing in bog areas do not seem to be adequate to account for the presence or absence of bog plants or their xerophilous structures. Experiments suggest, however, that farther north this factor is of prime importance.

In texture the bog substratum shows every gradation from the coarse fibrous peat of the bog-sedge zone to the black powdery muck of cleared land. Bog soils in general do not afford as good a foothold for trees as do the mineral soils.

Peat is very resistant to the diffusion of mineral salts, hence bog

areas have a very different soil solution from that of the mineral soils adjoining. The high water capacity of peat is detrimental to plants, in so far as it prevents proper aeration of the substratum. Bog waters have no higher osmotic pressure than ordinary soil waters.

The absence of sphagnum from local bogs cannot be explained by the presence of calcium salts, as shown by observation, chemical analyses, and experiments.

The acidity of local bog water varies from .00015 to .00258 normal acid. The lowest values are found in areas covered by bog sedges and swamp plants, and they are approximately the same. The highest occur under the tamaracks. The variations in acidity are related inversely to the temperature. As shown by experiment, this is because of increased oxidation at the higher temperatures. It is suggested that we should find increased acidity as we go north. There is no apparent relation between color and acidity, except that light colored waters usually show slight acidity. The acid nature of the soil solution is a factor in the competition between different species for the occupancy of bog areas.

Bog soils are notably deficient in potassium and available nitrogen. Nitrifying bacteria are prevented from carrying on their normal activities by the acidity of the soil solution, by the lack of oxygen, and by the lower temperature of the substratum.

With few exceptions bog plants are light-demanding forms; hence, in their competition with one another, size and shading ability are prime factors.

That the conditions in the Huron valley are at present not as favorable to the bog plants as to the swamp plants, is shown wherever the two societies come into competition. This fact must be contrasted with the situation in the optimum region of the distribution of bog plants, where the opposite relation has been shown to exist.

An examination of all the physical and chemical data now available fails to account for the differences in flora of bog and swamp areas in this region. The most important factor is believed to be their physiographic history. Where the habitat dates back to Pleistocene times and has remained undisturbed, we find today the bog flora. Where the habitat is of recent origin or has been recently dis-

turbed, we find the swamp flora, or mixtures of swamp and bog species.

The nature of the bog plant societies of the Huron basin is shown by the description of several local bogs, selected to show both the local bog flora and the variation in societies, and arranged to present the genetic changes in a bog flora as a basin filled by peat accumulation. It is shown that during the early stages of bog development, bog sedge, bog shrub, and conifer societies follow each other in the invasion of the basin. These several societies may vary considerably in composition, but they are closely related and show every gradation in a definite order of succession. The bog conifers, however, show no relationship to the surrounding broad-leaved forests of the upland. On the other hand, where clearing has occurred, swamp sedges, swamp shrubs, and swamp trees gain the ascendency, and these not only show an order of succession among themselves, but are genetically related to the broad-leaved trees of the region. The bog societies are part of the northeastern conifer forest formation, while the swamp societies are related to the southeastern broad-leaved forests.

An anatomical study of the bog plants shows that epidermal and hypodermal tissues are thick-walled, that a heavy cuticle is present, frequently supplemented by wax and hairs. Resinous bodies are to be found in the roots and leaves of many of the plants. The leaves are usually small and revolute-margined. Palisade tissue makes up a large part of the mesophyll. Mycorhizas are present in most of the plants. Bog plants resemble the plants of dry sand plains in reduction of foliage area, in development of protective coverings for above-ground parts, and in palisade tissues, but differ from the latter in the matter of root development and root structures.

Experiments indicate that the local bog water itself has no tendency toward the production of xerophilous modifications. Low soil temperatures and lack of soil aeration, however, cause a reduction in the development of the several plant organs. When these two factors are combined, the effect is very marked.

Experiments with *Rumex acetosella* are of especial interest in that nearly all of the characteristics of bog plants may be developed either by lowering the soil temperature, as compared with the air temperature, by preventing proper soil aeration, or by growing in

dry sand. Palisade tissue was developed in the leaves of these plants in diffuse light, and it is shown that palisade tissue is to be correlated with physiological drought. An analogy between the bog habitat and the dry sand habitat is established.

Experiments with Larix indicate that mycorhizas develop only in poorly aerated substrata; their growth is exceedingly slow; the acidity of the substratum is not a factor in their development; a naturally or artificially aerated substratum favors the development of normal roots, and these roots when not surrounded by water develop root hairs abundantly. Larix seedlings can withstand prolonged submergence. When exposed to low substratum temperatures and poorly aerated soil conditions, Larix produces more xerophilous leaves.

Further field work on the bog plant societies needs to be carried on in the region extending from Winnipeg to New Brunswick. Data on the soil and air temperatures, the acidity, the chemical composition of the soil solution, and the plants associated in bog areas throughout this region will go far toward solving the problems of the distribution of bog plants. Experimentation on the production of xerophilous structures by bog conditions should be continued on a larger scale than is possible in the ordinary university plant-house.

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UNIVERSITY OF MICHIGAN.

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NUCLEAR DIVISION IN ZYGNEMA.

MABEL L. MERRIMAN.

(WITH PLATES III AND IV)

THE species of Zygnema chosen for this investigation possesses a nucleus unobscured by chromatophores, and hence one in which division stages can be easily followed. No zygospores were found in the material, so the species could not be identified with any degree of accuracy. The number of pyrenoids are normally two, one on each side of the nucleus. The material was gathered from the same locality, the margin of a brook, during the months of August and September of two successive years. The filaments were studied in a living condition to make sure of the presence of dividing nuclei, and were then killed in chromacetic acid and the weaker solution of Flemming for later study. The greater part of them were killed in the evening, as it was also desired to secure division stages of other Conjugatae, which grew in great abundance in the locality and have been reported by investigators as dividing more actively at night. Of these, three species of Spirogyra and two of Mesocarpus will furnish the material for a later contribution.

As nearly all the literature upon the cytology of the Conjugatae relates to forms of Spirogyra, its consideration will be deferred until the completion of further studies in the nuclear division of the group. It is hoped then to bring into accord all the observations as to the character of chromatin and nucleoli.

Filaments of Zygnema treated with the combination stain of safranin and gentian violet, were found upon examination to have retained the violet only in the cell sheath, while the nuclear structures and pyrenoids retained the safranin. Various results were obtained with those treated with Heidenhain's haematoxylin in combination with iron alum and eosin. As the same length of exposure to the stain did not suffice for Spirogyra and Mesocarpus growing entangled with the Zygnema, the material was allowed to remain in the staining fluids for a shorter or longer time. Filaments show pyrenoids stained black by the haematoxylin, the nuclear structures retaining the eosin; or the pyrenoids may be stained red by the eosin, and the

nuclear structures black by the haematoxylin; or finally both may appear stained red by eosin. Such differences are shown in the drawings from the different preparations; the parts shaded in black represent portions stained by the haematoxylin, as in *fig. 33*, those in gray the portions stained by the eosin, as in *fig. 13*.

Within a quiescent nucleus situated between the two pyrenoids thus stained, there can be seen a central body stained somewhat redder or blacker, as the case may be, than the peripheral network of granules. This network of granules, ordinarily scarcely distinguishable from the cytoplasmic reticulum, was found in some cases to be quite conspicuous.

If an examination is made of a nucleus in process of reconstruction from the telophase, within the forming membrane can be seen a conglomerate mass of substance, very evidently non-homogeneous both in surface view and as seen in outline, *figs. 1, 39*. Around this smaller bodies can be seen in the meshes of a delicate network. The staining capacity of the larger mass and the small bodies varies in the different preparations; in some instances they are sharply defined from one another, at other times they retain the same kind and amount of stain.

It cannot be denied, however, after a careful examination of stages preceding the appearance of these bodies, that the substances in both came from the chromosomes of the metaphase. Bearing in mind, then, that the large mass and the smaller granules have the same origin, it would hardly seem correct to discriminate between the two, terming the one nucleolus and the others chromatin granules. Neither method of staining nor study of their history yields evidence other than that they are of similar substance, differing only in position and aggregation. It is as if in the revolutions going on within the cell some of the chromatin granules had been drawn to the center, there incompletely cohering, while others were left at the periphery. In describing, then, the quiescent nucleus of Zygnema it seems preferable to say that the larger portion of the chromatin granules cohere to form a central body analogous in its position to the nucleolus of higher plants.

The division of the nucleus is presaged by granules collecting in the region where the cell wall will form. The activity of these vibrat-

ing granules in the living cell renders the nuclei about to divide easily distinguishable from the remainder in the filaments. Owing to the activity of these granules, changes going on within the living nucleus could not be easily followed, but changes in the form and position of the nucleus together with those of the pyrenoids were followed throughout division. Accordingly the history of changes in the chromatin is all deduced from comparison of dividing nuclei stained by haematoxylin or safranin as outlined above.

If haematoxylin in combination with iron alum could be considered as an infallible criterion for distinguishing chromatic from achromatic material, and stages could be selected from material stained by one of the methods only, it would be an easy matter to trace the history of this central body originating from the chromosomes of the metaphase. Often, as in *fig. 2b*, numerous deeply stained bodies are to be seen lying in the space surrounded by a membrane, with no trace of chromatin bodies without. In the nucleus represented in *fig. 5*, in place of the central body several smaller bodies can be seen marked off from the eosin-stained bodies by the blackness of the stain. Passing to *fig. 9*, where the beginnings of an intranuclear spindle are manifest, and where there are several more deeply stained bodies, and then to *fig. 12*, where six discrete bodies distinctly form an equatorial plate, the natural conclusion, based wholly upon similar staining properties, would be that the central mass of chromatin alone furnishes the chromosomes for the equatorial plate. Such was the conclusion reached during the first year of this investigation, but further study of the material shows it to have been premature, or, if applicable at all, only to a few cases. The conviction that difference in staining of nuclear structures is more often a matter of manipulation than of chemical reaction, and that difference in the shade produced by the stain is merely due to the density of the body and time given for penetration, renders necessary in interpretation a great degree of caution.

The following account is derived from a comparison of parallel stages in all the preparations.

As the nuclei pass from the quiescent to the active state, the centrally lying mass disintegrates into small bodies (*figs. 2, 3*); at the same time the granules lying at the periphery increase in size. The

space within the nucleus becomes gradually clearer (*fig. 5*), the nuclear sap probably reinforcing the substance of the granules. As the result of the disintegration of the central body and the growth of the other granules, there may be seen lying within the nucleus twenty or more granules (*figs. 4, 5, 6*). In a few cases these bodies may slightly cohere, but in the majority of cases they lie free. No cases were found here or in later stages of the formation of a spirem. In many instances all the bodies within the nucleus retained merely the eosin stain (*fig. 6*), and hence were entirely undifferentiated from each other. In a few cases, like *figs. 5, 7, 8*, some of the bodies retained only the black stain from the hæmatoxylin. In one instance (*fig. 11*), a faintly stained larger body, with one or two smaller ones of similar shade, can be seen lying within the nuclear space, surrounded by numerous more deeply stained granules. If the other stages mentioned had not been observed, the latter faintly stained body might have been interpreted as a nucleolus like those in higher plants, now in the act of becoming dissolved in the cytoplasm. Extended comparison, however, of parallel stages justifies the view that this body is only a portion of the central mass of the quiescent nucleus, about to undergo still further disintegration into chromosomes.

The many chromosomes thus resulting approach one another (*figs. 6, 9*), presenting in many cases an appearance analogous to the synapsis stage described as occurring in the higher plants. Finally they become arranged in a circle concentric with the short axis of the cell. In one case (*fig. 10*), such an arrangement was observed before the nuclear membrane became dissolved. *Fig. 14* shows this massing of granules in the equatorial plane after the dissolution of the nuclear membrane. The chromosomes in this cell were all stained black, but some were drawn in lighter tint to show that they were lying in three different planes. *Fig. 15* also represents a similar stage, and *fig. 18* one somewhat further advanced. The chromosomes now appear to be denser than in previous stages, an interpretation based upon the circumstance that the hæmatoxylin stain does not as readily become washed out.

After having formed the ring they appear to be drawn inward, becoming denser and undergoing a process of fusion. By this draw-

ing-in process they come to lie in two closely adjoining parallel rows. As no case of a single row of isolated granules in the same plane was found, there is no evidence that such double row was produced by the division of a single row. *Fig. 25* represents two rows of chromosomes lying in the same plane. In *fig. 12* fusion has taken place to such an extent that only three chromosomes are present in each row.

Many of the chromosomes presented a tetrahedral appearance, as in *figs. 16* and *20*, thus pointing to the conclusion that the fusion of the condensing granules may take place in fours. In some cases the fusion has gone so far as to result in only four groups of tetrads (*figs. 22, 23, 21*). *Fig. 24*, of a more highly magnified group, shows especially distinctly this grouping of the granules. Careful focusing on this stage indicated the presence of another underlying group. As many cases were found of such grouping of the chromosomes in fours, it does not seem that it could have been purely accidental.

When the maximum amount of fusion and condensation is reached, the limit apparently varying in different cells, each half of a group becomes dissociated from its adjoining members and gradually draws away, as in *fig. 27*. In process of separation each group becomes broken up into smaller groups, in the meantime all becoming again arranged in two rings concentric with the short axis of the cell (*fig. 26*).

Thus numerous chromosomes are arranged in a circle in stages preceding and immediately following the stage of the equatorial plate, in which commonly four to six chromosome groups may be seen. It seems difficult to believe that six chromosomes (*fig. 12*) could have resulted directly from condensation and fusion of thirty or more chromosomes (*fig. 14*). A comparison of chromosomes as to size and staining qualities in the two adjoining cells (*figs. 12, 13*), drawn with Abbé camera, would certainly indicate that each chromosome must suffer a loss of its more liquid substance in the process of being drawn into the equatorial plate, or that a few must be entirely dissolved. Whether all condense to form a few, or whether only a few are chosen to transmit the chromatin to daughter nuclei, the remainder becoming dissolved in the cytoplasm, cannot be stated with certainty, as the staining process does not solve the problem as to the fate of the individual granules. When *all* the preparations are

examined and not a selected few, there seems to be more evidence of the first being the true account of events.

It was thought at first that this difference in number of chromosomes might be due to difference of species, as none of the Zygnema examined had zygospores, and hence it is possible that two or more species might have been growing together. The discovery of cells like those in *figs. 6, 12, 13, 15, 23, 22*, in the same filament is indisputable evidence that in the same individuals the number of chromosomes decreases from thirty or more down to six or eight, and then increases to thirty or more. This change in number occurs in a few moments, as determined in living cells by the changes in the position of the nucleus. All the filaments were examined in surface view, so it cannot be maintained that the number of chromosomes had been increased by sectioning.

As the rings of chromosomes approach the chromatophores, the cytoplasm is condensed on the side nearest the chromatophore. The explanation of this might be that a large part of the cytoplasm which is not diverted to the region of the formation of the cell plate was streaming in toward the center, as in *figs. 14–18*, while in *figs. 26–30* it was streaming out towards the chromatophores; that the chromosomes are forced together by the inflowing streams and in the vortex of opposing currents become dissociated. The word "dissociated" is used in preference to the word "splitting," as there appears to be no evidence of splitting and hence of equal distribution of homogeneous bodies. The chromosomes being heavier than the cytoplasm, the condensation appears on the side nearest the chromatophore (*figs. 28, 29*).

It is to be regretted that in the living cells chromosomes could not be distinguished from actively vibrating granules in the cytoplasm. Nothing could be discovered which in any way resembled spindle fibers, although streams of granules and the alternating space of nuclear activity was easily traced.

The number of chromosomes finally arriving at the chromatophore may be fifteen to twenty in each ring, as in *fig. 30*. The cytoplasm, being somewhat arrested in its flow by the chromatophore, causes a change in the position of the chromosomes. The majority, as they undergo still further dissociation, are drawn to the center, incom-

pletely cohering, while a few appear lying in delicate strands about them (*fig. 31*). In some cases all the chromosomes may cohere to form the central body. The nuclear membrane now emerges from the condensation of cytoplasm (*fig. 32*). As the chromosomes are now shut off from the influence of currents in the cytoplasm they generally remain unchanged in position, fusing either to form one mass (*fig. 33*), or three or more smaller masses (*fig. 34*), or rarely (*fig. 35*) all the chromatic material may be diffused in the nuclear plasm, forming numerous more or less tetrahedral granules.

It is to be noted that not until the chromatic rings have separated and have approached the chromatophores do the pyrenoids ordinarily show any evidence of division. This observation was easily confirmed from the study of living cells. *Fig. 29* represents the only one seen, out of many filaments examined, in which the pyrenoids divided before the formation of the nuclear membrane. As the newly divided nuclei approach their respective chromatophores, one or both plastids begins to show a constriction. This deepens until when the nuclei come to lie directly over, only a narrow band of less dense substance resembling linin connects the two daughter pyrenoids (*figs. 37, 38*). This becomes gradually reduced until it appears only as a thread (*fig. 39*). Later the nucleus sinks down and the separation is complete. The constriction of the plastids forming the center of the two pyrenoids takes place synchronously, as is the case with the stages in the daughter nuclei. One instance only was observed in which one plastid suffered division when other plastids had just begun to elongate (*fig. 32*).

Although division of the pyrenoid may be influenced by division of the nucleus, that it is not wholly dependent upon it was demonstrated by leaving actively dividing filaments of Zygnema for one hour in a watch crystal containing 10^{cc} of water to which two drops of chloroform were added. There were but few visible signs of plasmolysis in filaments killed and stained as in other material, but while a majority of the nuclei had ceased to divide, a majority of the pyrenoids were dividing as in normal filaments. That this division was not merely fragmentation was shown by sequence of stages and the presence of the band connecting the plastids. Fragmentation of the pyrenoids took place in filaments in stronger solutions of water

and chloroform in which plasmolysis occurred to a much greater extent.

Hence, cytoplasmic streams, nuclear structures, chromatophores, and pyrenoids take an active part in the division of cells in Zygnema. The streams of granules, collecting where the cell plate is to form, marks the beginning; the nuclear changes then proceed, followed by division in chromatophores and pyrenoids, while all are correlative with the formation of the cell plate.

It cannot then be said that division of the nucleus, the chromatophores, and the pyrenoids are synchronous. Rather is it true that the center of activities of the cell shifts, and with this shifting division of the bodies lying in the vicinity occurs. As regards the nuclear structures in Zygnema it is apparent that there are no bodies analogous to the nucleoli found in the higher plants. A large portion of the chromatin, or in a few cases possibly all, fuses in the anaphase to form one or more bodies corresponding in appearance and position to that of nucleoli of higher plants. Instead of waste products of chromatin condensing to form one or more bodies in the nucleus, the waste products are not separated from the chromosomes, but retained in them until after the nuclear membrane disappears in the next division. The substances which make up chromosomes and nuclear waste products, if such we may rightly regard the nucleoli of higher plants to be, are in Zygnema morphologically indistinguishable.

The history of chromatin before the formation of the equatorial plate may be summarized as consisting of growth, association, and condensation of chromatin bodies in groups. These groups may be partially coherent, but in no case form a spireme. After equatorial plate formation, dissociation into groups follows, continuing until the chromosomes reach the chromatophores.

Although the term chromosome has been used in this account, researches as yet incomplete make it exceedingly doubtful whether the chromatin bodies in any of the Conjugatae are to be regarded as at all homologous with chromosomes of higher plants. If we restrict the term chromosomes to segments of the tubular spirem,[1]

[1] See MERRIMAN, Vegetative cell division in Allium, BOT. GAZETTE 37:178-207. *pls. 11-13.* March 1904.

then the chromatin bodies seen in *figs. 14* and *15* of Zygnema cells are homologous not with the chromosomes of Allium but with the granules seen in the earliest stage of the spirem, while groups in *figs. 16* to *23* are directly comparable with the groups or rings of tetrads, which in Allium fused to form the tubular chromosomes.

Zygnema possesses a mechanism of nuclear division less elaborated than that of the higher plants, inasmuch as dissociation of chromatin bodies occurs immediately after their association into primary groups without the intervention of a spirem. From this point of view appearances observed in Zygnema support the interpretation suggested in my account of nuclear division in Allium, namely, that the chromosomes are formed by fusion of bodies in groups, and that when a longitudinal splitting appears it is not to be considered a true splitting of a homogeneous substance but rather a dissociation of bodies which from the first were discrete.

If this be true, then doubts may reasonably be entertained as to the validity of the conception held by ROUX, and successively by many other investigators, that the complex apparatus for indirect division of the nucleus exists for the purpose of enabling each chromatin body to furnish its quota to the daughter nuclei.

The essential feature of indirect division, and therein its advantage over direct division, appears to be the dissolution of the nuclear membrane. Thus is made possible a free interchange of nuclear and cytoplasmic substances and a renewal of the vitality of the cell.

Zygnema, then, may be considered as furnishing additional evidence of interchangeability of nucleoli and chromatin bodies, of variability in their number, and negatively as furnishing no evidence that equal distribution of chromatin is effected by either transverse or longitudinal splitting of homogeneous bodies. Nuclear structures, cytoplasm, pyrenoids, and chromatophores are transferred in equal amounts to the daughter nuclei and by a process differing not fundamentally in the result from that which would have been attained by direct division.

NORTHFIELD, MASS.

EXPLANATION OF PLATES III AND IV.

The figures were drawn with the aid of an Abbé camera.

PLATE III.

FIG. 1. Daughter nucleus from a cell where the cell plate is not yet completed. The nuclear structures in this cell retained the eosin stain, the pyrenoids black from haematoxylin. × 1750.

FIG. *2a*. Nucleus preparing to divide, showing growth of bodies in the peripheral network before breaking up of the central body. Pyrenoids and nuclear structures in this cell retained only the eosin stain. × 1750.

FIG. *2b*. Nuclear material stained black by the haematoxylin, all the chromatic material being apparently condensed in the space occupied by the central body. × 1750.

FIG. 3. Nucleus showing the breaking up of chromatin body and increase in size of the peripheral bodies. The pyrenoids retained the eosin stain; all the nuclear structures are stained black, several of them somewhat darker than the others. × 1750.

FIG. 4. Nucleus showing the beginning of the massing of the chromosomes, the nuclear membrane as yet undissolved, the granules in the region of the cell plate formation being conspicuous. Chromosomes black, pyrenoids red.

FIG. 5. Later stage, showing the clearing of the nuclear interior, recalling the synapsis stage described in higher plants. Pyrenoids red, several chromosomes black, remainder red. × 1750.

FIG. 6. Similar stage, very frequent; chromosomes numerous, massed together, all stained red. × 1750.

FIGS. 7, 8. Similar stages where there is no massing of the chromosomes. In 7, six chromosomes were stained black, others red. In 8 those stained black are grouped in one corner of the nucleus, those red are scattered. × 1750.

FIG 9. A stage where distinct lines of granules connect chromosomes with nuclear membrane. Four chromosomes black, others red. × 1750.

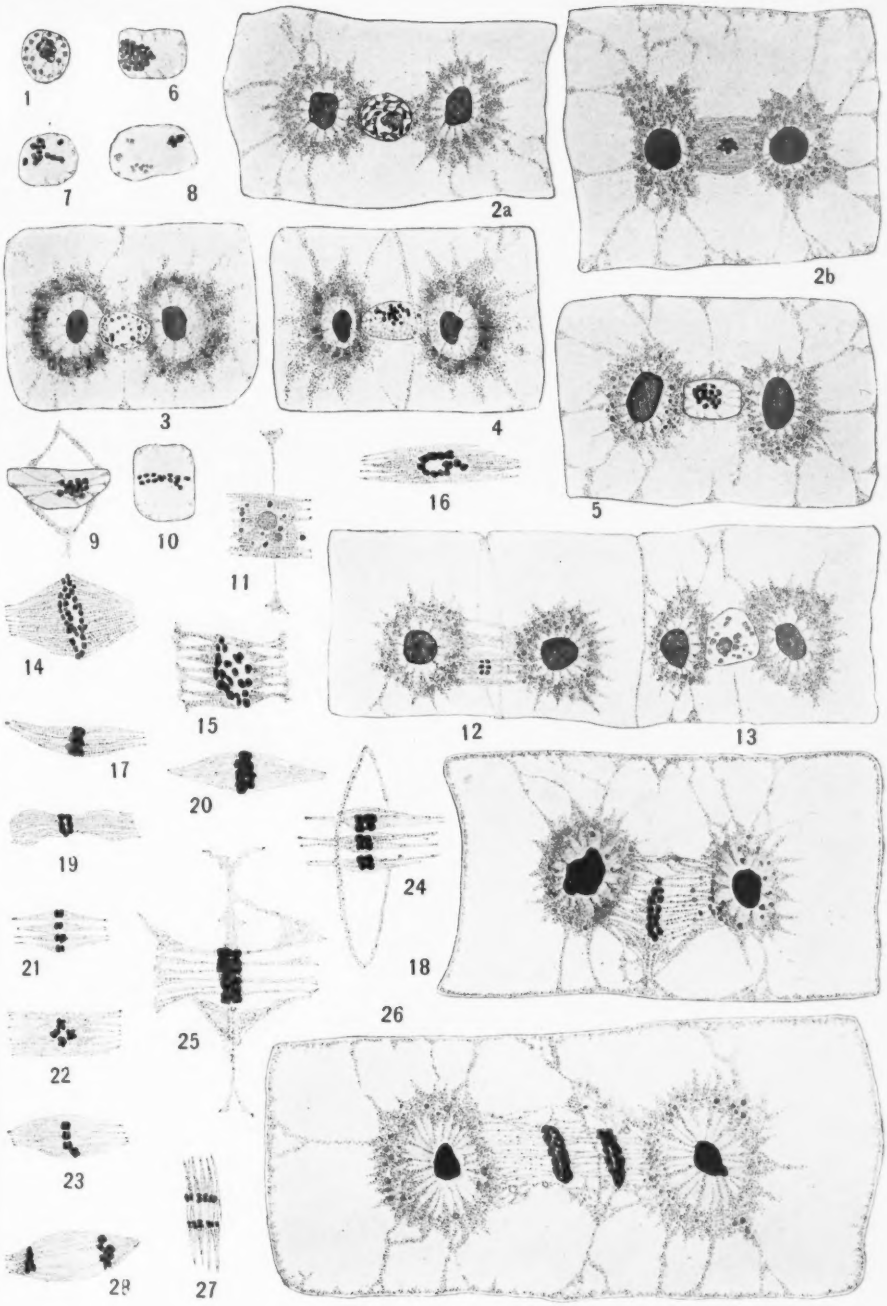
FIG. 10. A rare stage with numerous chromosomes arranged in circle within the nucleus before the nuclear membrane becomes dissolved. All chromosomes black. × 1750.

FIG. 11. Another rare stage; nuclear membrane dissolved, remains of central body still in the cytoplasm, retaining a lighter eosin stain than the other chromosomes. × 1750.

FIGS. 12, 13. Two adjoining cells in same filament showing disparity in size and number of chromosomes. Pyrenoids red, in *fig. 12* chromosomes stained sharply by haematoxylin; in *fig. 13* nuclear structures stained red. The line of granules marking the region of cell plate formation shown in both figures. × 1750.

FIG. 14. All chromosomes black, but some drawn lighter to indicate that they were lying in three different planes. × 2440.

FIG. 15. Chromosomes black, showing indefinite arrangement as they are being drawn to the center. × 2440.



MERRIMAN on ZYGNEMA

BOT

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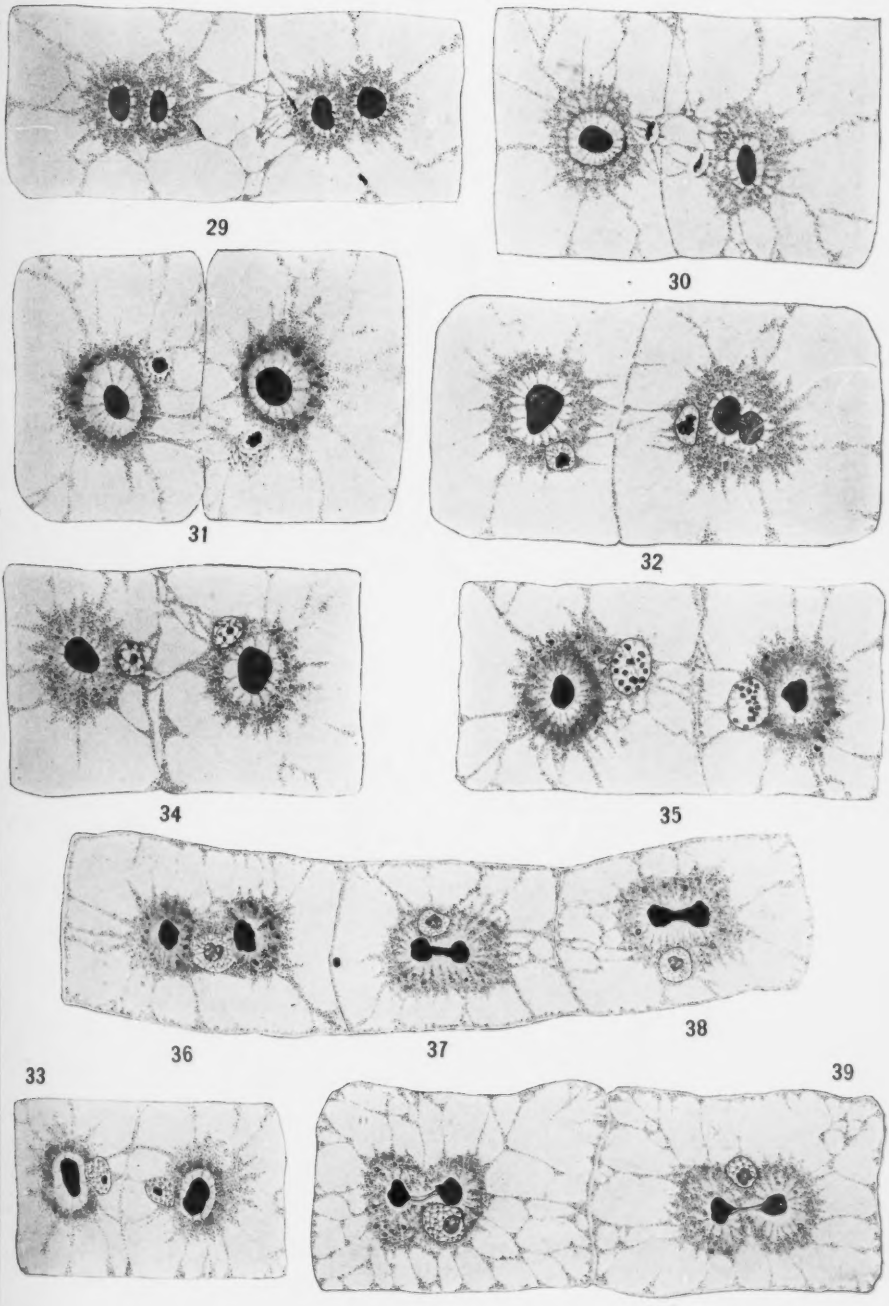

MERRIMAN on ZYGNEMA

FIGS. 16, 17, 19, 20, 21, 22, 23 show successive stages in condensation of chromosomes. Chromosomes all black. × 1750.

FIGS. 18, 24, 25, 26. Chromosomes and pyrenoids black. × 2440.

FIGS. 27, 28. Chromosomes becoming dissociated into smaller groups. Chromosomes black. × 1750.

PLATE IV.

FIG. 29. An unusual case of division of pyrenoids before formation of membranes of daughter nuclei. Chromosomes black, both in central mass and in the periphery, pyrenoids red. ×1750.

FIGS. 30, 31, 32. Chromosomes black, pyrenoids red. ×1750.

FIGS. 33. Pyrenoids and central body of nucleus black, peripheral bodies red. ×1750.

FIG. 34. Pyrenoids red, all the nuclear bodies black. ×1750.

FIG. 35. Nuclear bodies red, pyrenoids black. ×1750.

FIGS. 36, 37, 38. All nuclear bodies red, pyrenoids black. ×1750.

FIG. 39. Nuclear bodies red, pyrenoids black, showing vestiges of connecting substance. × 1750.

EFFECT OF CERTAIN SOLIDS UPON THE GROWTH OF SEEDLINGS IN WATER CULTURES.[1]

J. F. Breazeale.

(WITH FOUR FIGURES)

In certain investigations on the growth of wheat seedlings in aqueous extracts of soil, it was observed that the growth of these plants was greatly accelerated by the presence in the medium of undissolved calcium carbonate. That the observed acceleration was not due to an increase in dissolved calcium was apparent from the fact that the presence of other slightly soluble salts of this element failed to produce any response. It appeared possible that the effect of calcium carbonate might be due to its taking up some injurious substance present in the extract. This was suggested by Nägeli's well-known discovery[2] that water, which is toxic to algae because of minute traces of metals, can be improved by placing in it such insoluble bodies as graphite, paraffin shavings, or torn filter paper. It was determined to try other slightly soluble compounds which might remove from solution small amounts of solutes, either by chemical action or mechanically. The results of this investigation make up the present paper.

The Russian variety of wheat known as "Chul," obtained from Arizona, was used in most of these experiments. The seedlings were germinated in sand and then grown in water cultures in large-mouthed black bottles of about 600cc capacity. They were fixed in cork stoppers, four in a bottle, in the manner described by Whitney and Cameron[3] for cultures of this kind, so that the roots were submerged in the solution while the seeds were just above its surface. The solutions were always aerated by violent and repeated shaking before the cultures were started. During the growth of the plants the bottles were weighed in groups of three at intervals of three or four days, and the water lost was replaced with distilled water. The manner

[1] Published by permission of the Secretary of Agriculture.

[2] Nägeli, C. von, Ueber oligodynamische Erscheinungen in lebenden Zellen. Denkschr. Schweiz. Naturforsch. Gesell. **33**:1. 1893.

[3] Whitney, M., and Cameron, F. K., Investigations in soil fertility. U. S. Dept. Agric., Bureau of Soils, Bull. 23. 1904.

of fixing the seedlings practically prevents water loss, except through the transpiration of the plants. The work of LIVINGSTON[4] indicates that total loss by transpiration for a period of two or three weeks furnishes a fair criterion for comparison of the growth of different cultures of wheat grown in this manner. The transpiration figures are used in this way in the experiments here given. The work was carried on in a greenhouse with a temperature of 15 to 25° C.

For Experiments I to III a soil extract from poor Leonardtown loam, collected near Leonardtown, Md., was used. It was prepared by stirring the soil for three minutes with water in amount equal to twice its air dry weight, allowing it to stand twenty minutes, and then filtering through a clean Pasteur-Chamberland filter tube, in the manner described by WHITNEY and CAMERON.[5]

In Experiment I the solids used were calcium carbonate, tricalcium phosphate, ferric hydrate and aluminum hydrate. Ferric hydrate was prepared by precipitation from the chlorid with ammonia, followed by thorough washing with hot water. It was transferred moist to the culture media. Aluminum hydrate was prepared in a similar way from the sulfate. Data for this and the three following experiments are given in Table I. The percentage increase in transpiration for each solid is computed by considering the transpiration from the untreated extract as unity.

All of the solids accelerated growth, as is shown by the transpiration figures. But in the case of the ferric hydrate the root growth was accelerated to a much greater extent than that of the tops. The roots of the culture with this substance were much longer than those of the other cultures. It is evident here that root growth was accelerated without a corresponding increase in transpiration.

Experiment II comprised, besides calcium carbonate and ferric hydrate, carbon black (prepared from burning petroleum, and thoroughly washed), magnesium carbonate, and barium carbonate. The small amounts of water transpired are due to cloudy weather.

The plants of this series are shown in *fig. 1*, the numbers in the figure corresponding to the culture numbers given in parentheses

[4] LIVINGSTON, B. E., Relation of transpiration to growth in wheat. BOT. GAZETTE 40:178–195. 1905.

[5] WHITNEY, M., and CAMERON, F. K., The chemistry of the soil as related to crop production. U. S. Dept. Agric., Bureau of Soils, Bull. 22:16 ff. 1903.

in the table. It will be noticed that carbon black shows the same tendency to produce abnormal root growth as does ferric hydrate, but to a less marked degree.

Experiment III included very finely pulverized quartz flour, as well as ferric hydrate and carbon black. The two last named bodies showed here the same abnormal acceleration of root growth as was previously observed, but quartz flour, although it improved the general growth of the plants, produced no such effect.

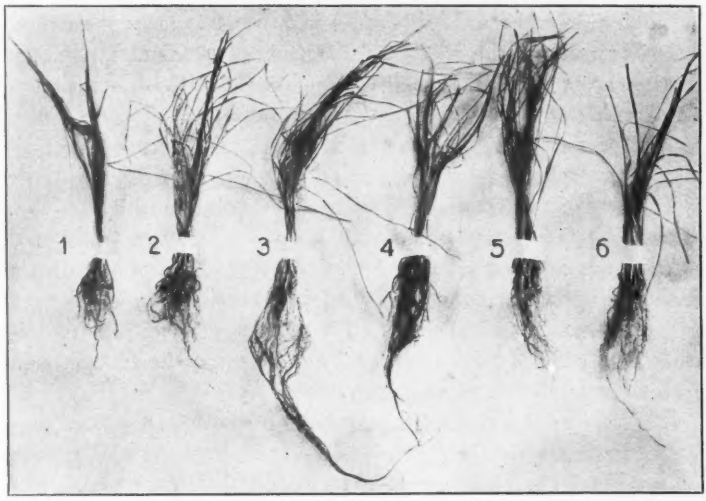

FIG. 1.—Experiment II; 24 wheat plants grown 19 days. 1, Extract of Leonardtown loam; 2, the same with calcium carbonate; 3, the same with ferric hydrate; 4, the same with carbon black; 5, the same with magnesium carbonate; 6, the same with barium carbonate.

The experiment with ferric hydrate and carbon black has been repeated many times with extract of Leonardtown loam, as well as that of other soils, and always with the same result. In some cases acceleration of root growth is more marked with carbon black than with ferric hydrate, but usually the reverse is true.

Experiment IV was carried out with an aqueous extract, prepared as above, from Miami silt loam collected at the Rhode Island Experiment Station, at Kingston, R. I. This soil had been in hoed crops

for ten years without fertilizer, and was acid to litmus paper. To make absolutely sure that the effect of carbon black was not due to any substance added with it, the distilled water for the soil extract was shaken with the solid carbon black and filtered through a

FIG. 2.—Experiment IV; 36 wheat plants grown 13 days. 1, extract of Miami silt loam; 2, the same with ferric hydrate; 3, the same with carbon black; 4, the same with ferric hydrate, carbon black, and calcium carbonate.

Pasteur-Chamberland tube before being used. Ferric hydrate, carbon black, and a mixture of these two bodies, together with calcium carbonate, were used in this case. The plants are shown in *fig. 2*.

From this experiment and others of similar nature it seems clear

that the effect of the carbon black is not due to any stimulating substance which it carries into the medium. Other experiments have shown that no acceleration of growth is obtained with the addition

TABLE I

DATA FOR EXPERIMENTS I TO IV.

Medium	Experiment I, 24 plants grown 19 days		Experiment II, 24 plants grown 19 days		Experiment III, 12 plants grown 17 days		Experiment IV, 36 plants grown 13 days	
	Total transpiration	Per cent. increase	Total transpiration	Per cent. increase	Total transpiration (av. of 2 cultur's)	Per cent. increase	Total transpiration	Per cent. increase
Untreated soil extract.....	154	....	(1) 33	....	51	....	(1) 68	....
Do. + tri-calc. phosphate..	182	18.1	....	....	....	....	....	....
Do. + calcium carbonate..	191	24.0	(2) 81	145.4	....	....	....	....
Do. + ferric hydrate.....	184	19.5	(3)110	233.3	187	266.6	(2) 176	158.8
Do. + aluminum hydrate..	187	21.4	....	....	....	....	....	....
Do. + carbon black	....	....	(4) 69	109.0	154	201.9	(3)139	104.4
Do. + magnes. carbonate..	....	....	(5) 73	121.2	....	....	....	....
Do. + barium carbonate...	....	....	(6) 78	136.3	....	....	....	....
Do. + quartz flour.....	....	....	....	....	87	70.5	....	....
Do. + ferric hydrate, carbon black, and calcium carbonate.....	....	....	....	....	....	....	(4)221	225.0

of iron salts to the extract of poor Leonardtown loam. Therefore, a slight increase in dissolved iron cannot be the cause of the acceleration noted in the case of this hydrate. It seemed probable that ferric hydrate and carbon black had their effect through an active removal, perhaps by mere adsorption, of some injurious substance occurring in the culture medium. Such a substance might have been in the soil extract originally, or might be produced by the plant roots, or both suppositions might be true together. The third alternative proved to be the correct one.

To obtain evidence in this regard, Experiment V was carried out. Four different soil extracts were shaken with carbon black, filtered, and then used as culture media, comparison being made with controls in untreated extracts. The four soils were of two types, a good and a poor soil of the Cecil clay type, and a good and a poor of the Leonardtown loam type, the former from Statesville, N. C., and the latter from Leonardtown, Md. Chemical analysis both of the aqueous extracts and of the solution obtained by digestion with hydrochloric

acid, fails to show any material difference between the good and the poor varieties of these soils, although they are agriculturally quite different. These cultures were grown under the direction of Mr. F. D. GARDNER, in charge of the Division of Soil Management, of this Bureau. They consisted of forty-eight plants and were grown for

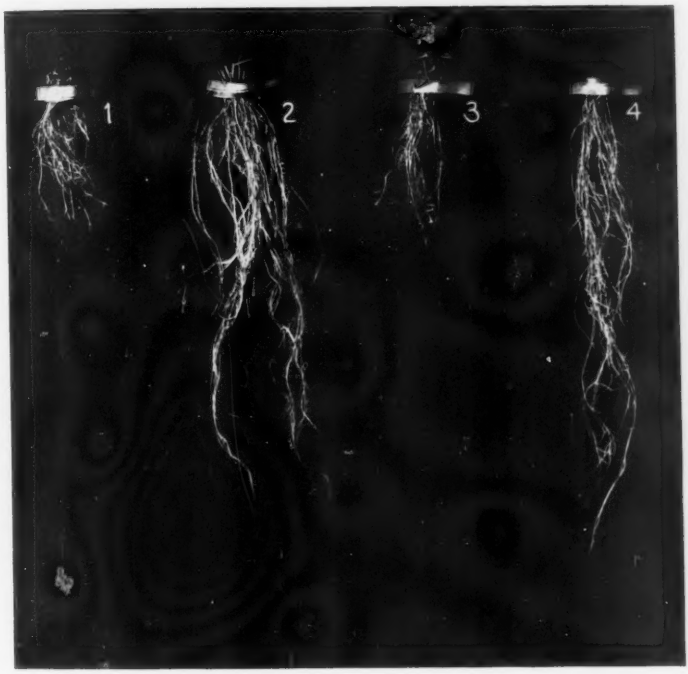

FIG. 3.—Experiment V; 48 wheat plants grown 15 days. 1, extract of Cecil clay, good; 2, the same, filtered from carbon black; 3, extract of Cecil clay, poor; 4, the same, filtered from carbon black.

fifteen days. The results are given in Table II; percentage increases are given for each treated extract compared with the same extract untreated considered as unity.

It will be seen from this table that the extract of good Cecil clay

TABLE II.

DATA FOR EXPERIMENT V.

Culture no.	Medium	Total transpiration in grams	Per cent. increase
1	Extract of Cecil clay, good	485	.....
2	Do., carbon filtered	471	−2.9
3	Extract of Cecil clay, poor	407	.....
4	Do., carbon filtered	477	+17.2
5	Extract of Leonardtown loam, good	359	.....
6	Do., carbon filtered	407	+13.4
7	Extract of Leonardtown loam, poor	271	.....
8	Do., carbon filtered	349	+28.7

was not improved by treatment with carbon where the latter is filtered out. All the others were improved, although the improvement in the case of good Leonardtown loam was not as marked as that in case of the poor. The leaf development and general appearance of the plants were essentially in proportion to their transpiration. The roots showed the same acceleration with carbon treatment and filtering that had been observed in experiments in which the solid was left in the solution. *Fig. 3* shows the roots of cultures nos. 1, 2, 3 and 4. From this experiment and from similar ones it appears that a part at least of the injurious matter which is removed by carbon black is in the soil extract at the start.

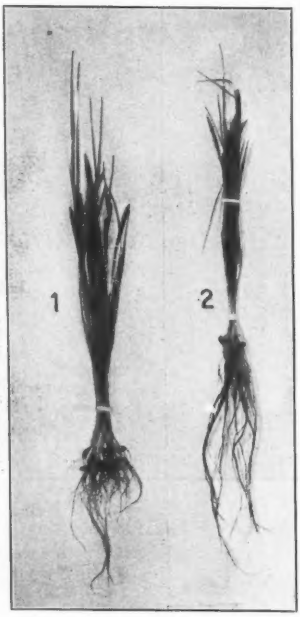

FIG. 4.—Twelve wheat plants grown 15 days. 1, redistilled water; 2, the same, with ferric hydrate.

A number of experiments were carried out, using water twice redistilled, first from potassium dichromate and sulfuric acid, then from alkaline potassium permanganate, both in glass boilers, con-

densation being carried on in a platinum tube. Upon this water the effects of carbon black and ferric hydrate were tested, the solids remaining in the water during the growth of the plants. The former gives little or no increase in transpiration, the latter a moderate increase, but both solids produce a marked acceleration in root growth. Twelve seedlings grown fifteen days in redistilled water with and without ferric hydrate are shown in *fig. 4*. No. 1 shows those from the untreated water, no. 2 those with the solid. The water here used probably did not contain injurious substances, and therefore the effect of the solids is most probably due to the removal of some injurious exudation arising from the plants. Further, distilled water in which plants have been grown for a number of days is found to give less growth upon replanting than does unused water, and the injurious effect of the used water is corrected by shaking with carbon black or ferric hydrate and filtering off the solid. Thus it seems that wheat seedlings do give off bodies from their roots which are toxic to themselves.

When the work so far recorded was practically completed, the appearance of TRUE and OGLEVEE'S paper[6] on somewhat similar experiments made it seem advisable to withhold publication until some further tests suggested by that paper could be made. These authors find that by the introduction of sand, filter paper, paraffin, or potato starch into solutions of copper sulfate in which seedlings of *Lupinus albus* are growing, the toxicity of the solute is remarkably decreased. By this means the killing concentration of the salt may be effectively reduced, according to the amount of the insoluble body present, either to a stimulating concentration or to one in which the physiological effect is not apparent. They reasoned that the solid absorbed the salt from the solution and in this way produced an effect closely paralleling that of simple dilution.

It was determined to test the effect of solids in solutions of sulfuric acid. Maize was here used instead of wheat. First, the strength of this acid necessary to prevent the growth of maize seedlings was

[6] TRUE, R. H. and OGLEVEE, C. C., The effect of the presence of insoluble substances on the toxic action of poisons. Science N. S. **19**:421–424. 1904. Also BOT. GAZETTE **39**:1–21. 1905. In this connection see also DANDENO, J. B., The relation of mass action and physical affinity to toxicity, etc. Am. Jour. Sci. **17**:437–458. 1904.

determined as lying between $n/2750$ and $n/3250$.[7] Then a series of varying concentrations of this acid on either side of the toxic limit was carried out, placing clear sand, quartz flour, filter paper, and paraffin shavings in the solutions. In no case was the apparent death limit modified by the presence of these substances. The death limit was also determined for a solution of sulfuric acid saturated with calcium sulfate, and for the same solution with an excess of calcium sulfate, but the solid again had no apparent effect.

With copper sulfate solutions carbon black was found to decrease the toxic effect, just as the authors above cited found to be true for the solids with which they worked. In order to bring out the effect of the carbon black, copper sulfate in the proportions of one and five parts per million of copper was added to the nutrient solution above described; a portion of the solution thus prepared was shaken with carbon black and then filtered, and wheat seedlings were grown in the treated and untreated solution. This series constitutes Experiment VI. Twenty-four plants composed a culture and the experiment lasted twelve days. The results are given in Table III.

TABLE III.

DATA FOR EXPERIMENT VI.

Culture no.	Medium	Total transpiration in grams
1	Nutrient solution	216.3
2	Do. + 1 p.p.m. Cu	67.3
3	Do. + 5 p.p.m. Cu	41.5
4	As 2, but carbon-treated	140.2
5	As 3, but carbon-treated	138.7

The growth of the plants was proportional to their transpiration. It is evident that the carbon removed sufficient copper to render carbon-treated solutions much less toxic than the untreated ones. This is a direct corroboration of the work of TRUE and OGLEVEE, but with another solid, and in this experiment the filtering out of the solid removes any possibility of its having any effect directly upon the roots. The explanation of these authors seems to be correct, as far as copper sulfate is concerned. The failure in the present

[7] This determination had been made previously, but was repeated for the present work. See CAMERON, F. K., and BREAZEALE, J. F., Toxic action of acids and salts on seedlings. Jour. Phys. Chem. **8**:1–13. 1904.

instance to get the same effect with sulfuric acid may be due to the fact that to be injurious this substance must be at a much higher concentration than is needed in case of the copper salt, while the relative amount of solute absorbed by solids is much greater in dilute solutions than in more concentrated ones. TRUE and OGLEVEE suggest this explanation for their failure to get marked improvement by the use of sand in solutions of phenol and resorcinol.

On account of the presence of toxic substances in distilled water as ordinarily prepared, from copper boiler and tin condenser, most workers with toxicity problems have used water redistilled in glass. In these laboratories the distilled water is often quite toxic to wheat seedlings, but its injurious effect is prevented if it is first shaken with carbon black or ferric hydrate and the solid filtered off. It is found that water so treated produces as good a growth of seedlings as does the most carefully prepared redistilled water.

It appears from these experiments (1) that extracts of certain soils are toxic to wheat seedlings in water culture, and that this toxicity is removed wholly or in part by carbon black, calcium carbonate, ferric hydrate, and other solids; (2) that the toxic substances of ordinary distilled water may be removed by ferric hydrate or carbon black; (3) that the roots of wheat seedlings give off substances which are toxic to themselves and that these substances can be made inactive by the presence of the last named solids in the culture medium; (4) that the presence of ferric hydrate and carbon black in the solution seemingly accelerates to a marked degree the development of roots, causing them to surpass the tops in growth.

The work here reported was done chiefly in the laboratories of the U. S. Department of Agriculture, Bureau of Soils, Washington, D. C. It was finished at the Rhode Island Agricultural Experiment Station, Kingston, R. I. I am indebted to Dr. F. K. CAMERON, and to Dr. B. E. LIVINGSTON, of the Bureau of Soils, for much valuable suggestion and advice.

U. S. DEPARTMENT OF AGRICULTURE,
Bureau of Soils,
Washington, D. C.

BRIEFER ARTICLES.

NOTES ON NORTH AMERICAN GRASSES. V.

SOME TRINIUS PANICUM TYPES.

BELOW are given a few notes upon certain species of Panicum described by TRINIUS from American material. The herbarium of TRINIUS, the father of modern agrostology, is deposited in the St. Petersburg Academy of Sciences. The curator of the herbarium, Dr. D. I. LITWINOW, very kindly sent, for deposit in the National Herbarium, portions of the specimens of the species mentioned in this article. It will be observed that three of the seven species had been described by earlier authors, while four have been recently described as new species. It must be said, however, that it would be impossible to identify any of these four species from the description alone. This is true of many of the earlier descriptions of the group *Dichotoma* of the genus Panicum, and on account of the difficulty of consulting the types of these species, it is in a measure excusable, on the ground of convenience, to describe unidentified species as new, without determining the application of the older names. Such painstaking and laborious comparison should not, however, be shirked by a monographer.

P. CHAMAELONCHE Trin. 1826, Gram. Pan. 242.

Palmare et minus. Panicula (semipollicari) lucidissima; Spiculis pusillis, obovato-oblongis, obtusiusculis, glabris; pedicellis hispidulis; Gluma inferiore flosculis triplo breviori 1-, superiore eosdem aequante 5-nervi; Hermaphrodito elliptico, mucronulato, laevi, neutrum aequante.

V. spp. Am. bor. (TRATTINICK, ex. coll. Enslini).

Plantula caespitosa, stricta, culmo tenuissimo, ramuloso. Folia lanceolata l. lineari-lanceolata, strictiuscula, semipollicaria, glabra; culmea et juniora subinvoluta, acicularia, breviora. Panicula pauciflora, tenera, prodit e summa vagina elongata, cujus folium eandem fere aequat. Flosculus neuter univalvis? Hermaphroditus albescens.

Label accompanying type specimen: "In Am. bor. s. dat. sine nom. ex. hb^{io} Enslini cl. Trattinick."

Specimen = *P. Baldwinii* Nutt. 1898. Scribn. Div. Agros. Bull. 11:43.

P. DEMISSUM Trin. Spec. Gram. **3**:319.

The type specimen is from Rio Janeiro. I have not seen this species from North America. It is mentioned here because the name occurs occasionally in the literature of North American grasses, and has been doubtfully applied to certain of our species.

P. ENSLINI Trin. 1826, Gram. Pan. 230.

Pedale. Panicula (subdigitali) contractiuscula, lucida; Spiculis subultralinealibus, ellipticis, acutiusculis, pilosulis: pedicellis glabris; Gluma inferiore flosculis sub 4-plo breviori 1-, superiore eosdem vix excedente 7-nervi; Hermaphrodito oblongo, acutiusculo, laevi, neutrum fere aequante.

An *Panicum tenue* Mühlenb. (quod *Pan. liton* Schult. Mant. 2. p. 250) quaerit ill. N. AB ESENB. in litt.

V. spp. Am. bor. (TRATTINICK, e collect. Enslini.)

Culmus basi ramosus, ad paniculam usque vaginatus: vaginis arctis, fissura pubescentibus. Folia glabra: radicalia lanceolata-oblonga l. ovata, sesquipollicaria, lineas 4–5 lata; superiora lineari-lanceolata, duplolongiora, patentia. Panicula e summa vagina prodit radiis subcapillaribus, parum patulis. Gluma inferior epilis, superior mucronulata cum flosculi neutrius valvula inferiore pilis adspersa. Hermaphroditus albescens.

Label accompanying type specimen: "(an *Pan. tenue* Muhlb. quaerit NEES AB ES.) ab Enslino in Am. bor. l. dt. sine nom. cf. Trattinick Wiennae 1820."

Specimen = *P. equilaterale* Scribn. 1898, Div. Agros. Bull. 11:42.

Characterized by having the spikelets of *P. commutatum* but the leaves elongated and widely spreading.

P. FLORIDANUM Trin. 1835, Mem. Acad. Petersb. VI. 3^2:248.

The type specimen from Georgia is *Paspalum racemosum* Nutt. = *P. bifidum* (A. Bertol.) Nash, as has been generally recognized.

P. JEJUNUM Trin. 1836. Bull. Acad. Petersb. 1:76.

The type specimen from Louisiana sent by Hooker in 1835 is *Panicum hians* Ell. = *Steinchisma hians* (Ell.) Nash.

P. LANCEARIUM Trin. 1822, Clavis Agros. 234.

1179. Gr. miliaceum americanum, minus, panicula parva. *Pluk. Phyt.* p. 176. *Tab. 92* f. *6*.

Mor. p. 197. no. 15. Panicum lancearium *m.* (*de quo alio loco*).

Label accompanying specimen: "Plukn. Tb. 92 f. 6.? In Am. bor. ab Enslino l. dt. cl. Trattinick."

Specimen = *P. Nashianum* Scribn. 1897, Div. Agros. Bull. 7:79.

The specimen matches *Curtiss 4029* from Florida, the first specimen cited in the original description of *P. Nashianum*. Both have glabrous spikelets. The second specimen cited by SCRIBNER, *Nash 466*, from Florida (the type on account of the specific name), has pubescent spikelets.

Since TRINIUS gives a binomial to a plant described by PLUKENET and by MORRISON under a polynomial designation, PLUKENET'S plant is the type.

In Kew Index *P. lancearium* is cited as Agrost. Bras. 246. The name

is mentioned in that work (NEES, 1829, Agrost. Bras. 226) in a note appended to *P. parvifolium* Lam., where it is referred to *P. angustifolium* Ell. It is quite distinct from ELLIOTT'S species, however.

TRINIUS himself describes the species later as follows (1826, Gram. Pan. 223:)

Spithamaeum. Panicula (vix pollicari) lucidissima; Spiculis parvis, obovatis, glabris: pedicellis scabriusculis; Gluma inferiore flosculis triplo breviori enervi, superiore eosdem aequante 7-nervi; Hermaphrodito oblongo, acutiusculo, laevi, neutrum aequante.

V. spp. Am. bor. (TRATTINICK ex hb^io. Enslini).

Ima basi in ramos discedit simplices, tenues attamen firmos, satis multi-(sex-)folios. Folia lanceolata, pollicaria, sensim breviora, praesertim basin versus ciliatula. Panicula e summa vagina prodit satis pauciflora, lineari-oblonga. Flosculus neuter bivalis. Hermaphroditus albens.

Since PLUKENET'S figures of this and the next cannot be identified, TRINIUS' specimens should be taken as the substitute type of these two species.

P. LEUCOBLEPHARIS Trin. 1822. Clavis Agrost. 234.

1177. Gr. miliaceum americanum, majus, panicula minore. *Pluk. Phytogr. p.* 176. *Tab.* 92. *f.* 7. *Mant.* p. 95. (*excl. Syn. Sloan. ut. ipse Sloaneus monet*). *Citatur a Gronowio* (Virg. p. 12.) *ad* Pan. paniculatum floribus muticis; *sed quid illud? Figura bene convenit cum Panico quodam herb. notsr. ex Amer. bor.* (Pan. leucoblepharis *m.*) *praeter cilia foliorum elegantissima, rigidiuscula.—Synon. Recchii ap. Pluk. admodum dubium.*

Label accompanying specimens: "ab Enslino in Am. bor. l. dt. cl. Trattinick."

Specimen = *P. ciliatum* Ell. 1816. Sketch 1:126.

Like *P. lancearium* the name is founded upon a figure in PLUKENET and is further described by TRINIUS in Gram. Pan. 219. 1826.

Spithamaeum et minus. Panicula (ultrapollicari) lucida; Spiculis subparvis, obovato-oblongis, pilosulis: pedicellis scabriusculis; Gluma inferiore flosculis plus duplo breviore 3–5, superiore eosdem aequante 7-nervi; Hermaphrodito oblongo, obtusiusculo, scrobiculato-punctato, neutrum aequante.

V. spp. Amer. bor. (TRATTINICK e plantis Enslini).

Basi ramosum. Folia cordato-lanceolata, amplexicaulia, pl. min. pollicaria, pallide viridia (plerumque elegantissime), pectinato-ciliata. Vaginae superiores elongatae. Axis pilosus. Gluma inferior epilis. Flosculus neuter bivalvis.

P. ciliatum is characterized by the ciliate but otherwise glabrous leaves and pubescent spikelets a little less than 2 ^mm long.

P. UNCIPHYLLUM Trin. 1826, Gram. Pan. 242.

Spithamaeum-pedale. Panicula (1-sesqui-pollicari) lucidula; Spiculis mini-

mis, oblongis, pilosis: pedicellis glabriusculis; Gluma inferiore flosculis triplo breviori 1-, superiore eosdem aequante 7-nervi; Hermaphrodito elliptico, laevi neutrum aequante.

Panicum laxiflorum Spreng. in Mém. de St. Pétersb. II. p. 291.

Panicum heterophyllum Mühlenb. teste N. ab Es.

V. spp. Am. bor. (TRATTINICK).

Culmus tenuis, adscendens, basi ramosus. Folia, quorum plura basi plerumque confertissima, lineari-lanceolata, cum vaginis pubescentia, pollicaria, lineas 2 lata: superiora angustiora, dissita. Panicula ovata, axis radiisque glabris. Flosculus neuter bivalvis. Hermaphroditus albescens.

Label accompanying type specimen: "Pan. heterophyllum Muhl. (Test. Nees) an Pluckn. Tab. 92 f. 8? ex herb Enslini, spmna Am. bor. Trattinick."

Specimen = *P. columbianum* Scribn. 1897. Div. Agros. Bull. 7:78.

In recent works this name has been applied to a species of the *lanuginosum* group having rather stiff foliage and the leaf blades hirsute on both surfaces. The true *P. unciphyllum* is easily recognized by the short crisp pubescence and the very short ligule, characters not mentioned in the original description.—A. S. HITCHCOCK, *U. S. Dept. Agric., Washington, D. C.*

SPOROGENESIS IN PALLAVICINIA.

THE August number of the BOTANICAL GAZETTE contains a paper by Mr. A. C. MOORE on *Sporogenesis in Pallavicinia*. I regret again to ask for space on this matter, but Mr. MOORE has so completely (though of course inadvertently) misrepresented my own position with regard to the nature and the significance of the quadripolar spindle in the Jungermannieae, and further, the grounds on which he founds his criticism appear to me to be so open to objection, that I venture to ask for an opportunity of replying to his strictures.

Firstly, then, as to the significance attached to the quadripolar spindle in 1894–5.

From Mr. MOORE's account it would seem that I regarded, as the most essential feature of its importance, the simultaneous distribution of the chromosomes of the dividing nucleus of the mother-cell to the four spores that are finally produced.

I certainly believed that in *Pallavicinia decipiens* such a distribution occurred, and that it resulted from the suppression of the period of rest normally intervening between the first and second maiotic divisions. In this I may be right, or further investigations may show that, in the species in question, I missed the binucleate stage, But this is really not the

essential matter at all. The result of my work published in 1895 went to show that in most forms there are two consecutive mitoses, the second, following more or less rapidly on the first, and I believed that in *P. decipiens* the brief interval might be so shortened as to have become practically obliterated.

But the circumstance that quadripolar spindles were shown by me to be plainly visible in properly fixed material of forms in which no such extreme telescoping of the normal sequence of events takes place, clearly proves that, whatever the significance of the quadripolar spindle may be, it certainly is not *essentially* related to a simultaneous distribution of the chromosomes amongst four daughter nuclei, and I never thought it was.

What I believed in 1895 (and I have seen no reason to materially alter my view), was expressed as follows: "The quadripolar spindle, then, is only a special case of ordinary karyokinetic phenomena; instead of two relatively large masses of protoplasm there are four distinct aggregations, one in every lobe, each exercising an independent strain, and the direction of the strains may continue separate to the very end of the process or not, according to the form and special circumstances of the cell."[1] I may perhaps add, that the principal importance of the phenomenon, in my view, lay in its bearing on the permanence of the centrosomes, at that time a widely accepted doctrine.

In the second place, Mr. MOORE seems to think that his observations on *P. Lyellii* vitiate the conclusions based on a study of *P. decipiens*. I venture to think they do nothing of the sort. It is clear that the two species differ in the form of their spore mother-cells to a marked degree, and also that this difference is exactly of a nature to account for the unequal persistence of the peculiarities of the spindle in the two cases. For the lobing of the spore mother-cell is so much less in *P. Lyellii* than in the other species, that it would be a matter for surprise if the quadripolar character of its spindle were so long retained.

I confess, however, that I should have expected centrospheres to be present at the stages represented in *pl. III, figs. 1–3* of Mr. MOORE'S paper. They are so obviously demonstrable in *Aneura pinguis* and in *Fossombronia pusilla*, the spore mother-cells of which resemble in their lobing those of Mr. MOORE'S plant.

One feels a little difficulty in repressing a suspicion as to the successful fixation of his material, a suspicion not dispelled by the further contemplation of *figs. 12* and *13*. They so faithfully depict preparations I have

[1] Annals of Botany **9**:508.

myself very often obtained when the fixation had been imperfect. It is, of course, easy in these plants to secure admirable preparations of the stages preceding and following on the maiotic divisions, but I am sure Mr. MOORE will agree with me as to the great difficulty encountered in successfully fixing the cell contents at this critical period. Personally, I have not found chromacetic acid (the fixative used by him) very successful, but obtained far better results with Flemming's solution and, if due precautions are taken, with acetic alcohol. The latter, in particular, has yielded results of especial excellence, owing partly, no doubt, to the relative rapidity with which it traverses the somewhat impervious cell wall.—J. B. FARMER, *Royal College of Science, London.*

REPLY.

PROFESSOR FARMER acknowledges that in 1894 he believed in the simultaneous distribution of the chromosomes to the four spores in *Pallavicinia decipiens*. His description stands as the only account of a process without parallel in the plant kingdom, and he must have realized its exceptional nature. The account became all the more remarkable when Professor FARMER'S own studies on a number of liverworts, published in the following year, showed two successive mitoses in the spore mother-cells as in other groups of plants. He acknowledges now that he may have missed the binucleate stage. This is precisely what I believe he did, but since I have not investigated *P. decipiens* I cannot assert that he did so. Now he states that this simultaneous distribution is really not the essential matter at all. Apparently the essential matter to him is his observation that several liverworts conform to the normal sequence of nuclear division during sporogenesis. Yet these conclusions, bearing as they do on *Pallavicinia decipiens*, served to emphasize the peculiarities of that account, and I feel confident that most, if not all, cytologists would pick out the description of a simultaneous distribution of chromosomes as the most essential feature of his paper of 1894.

I venture to think that botanists are not so much interested in the explanations which Professor FARMER may make of what he did or did not believe in 1894 and 1895 relative to the quadripolar spindle (which opinions they can form for themselves), as in the facts of sporogenesis in the liverworts. My study of *Pallavicinia Lyellii* is plainly a challenge of his account of *P. decipiens*, and together with Professor DAVIS'S work on Pellia, leads us to believe that the "quadripolar spindle" in all liverworts is a phenomenon of prophase followed by spindles of two successive mitoses, in essential agreement with the events of sporogenesis in other plants.

The reader must judge for himself whether it is at all likely that two species in the same genus should differ from one another so fundamentally as would appear from Professor FARMER'S description of sporogenesis in *Pallavicinia decipiens* and my own account of *P. Lyellii*.

Respecting the fixation of my material, I may say that I have no reason to think the penetration was not sufficiently rapid to fix the cell contents. Even with imperfectly fixed material my main conclusion is easily demonstrable, viz., that in *P. Lyellii* there are two successive mitoses in the spore mother-cell. Let us not lose sight of the main point at issue.—ANDREW C. MOORE, *South Carolina College, Columbia.*

CURRENT LITERATURE.

BOOK REVIEWS.

The algal vegetation of the Faeröese coasts.

BÖRGESEN'S extremely interesting account of the algal associations on the coasts of the Faeröe Islands,[1] is one of the most important contributions to the ecological side of marine botany. The work is a description of conspicuous algal associations along a varied rocky coast line, particularly favorable to algal vegetation, and is illustrated by more than thirty very excellent plates and figures from photographs. The factors affecting the algal vegetation are discussed; such as temperature and salinity of the water, tides and currents, wave action, temperature and humidity of the air, and light. The littoral and sublittoral floras are described, both for exposed and sheltered coasts, and also the floras of tide-pools and caves. A great many algal associations and formations may be clearly recognized in the Faeröes, some of them very conspicuous, as the Chlorophyceae formation, the Porphyra association, Fucaceae formations, Laminariaceae formation, and Alaria association. A particularly interesting chart plots the position of these associations in their position above and below the mean sea level.

It is extremely interesting to note that the cave flora is composed of forms of the sublittoral flora, which in the dim light are able to grow near the surface, or they are types which have the habit of growing in shaded situations outside. Littoral forms which grow in the brightest light are only found near the entrance of the caves. On entering a cave a condensed picture is obtained of the vertical distribution of algae from above downward. The forms in the deepest shadows are all red algae and some of them species which are usually found at great depths in the open sea. It is clear that light is the most important factor affecting the position of algal associations along a coast.

There is a detailed comparison of the algal flora of the Faeröe Islands with neighboring countries, Scotland, the Orkney and Shetland Islands, Norway, and Iceland, preliminary to a discussion of its origin. The flora had its origin from a mixture of Atlantic and Arctic species, which wandered northward with the retreat of the ice. Some of the arctic forms remained, adjusting themselves to the warmer waters, but there are many peculiarities of the algal flora which demand special explanations. BÖRGESEN does not believe that there were post-glacial bridges of land which made possible the migration of forms, but holds that factors now operative might have brought to the islands many algae from neighboring countries.

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[1] BÖRGESEN, F., The algal-vegetation of Faeröese coasts. Imp. 8vo. pp. 681–834. *pls. 13–24.* Copenhagen: H. H. Thiele. 1905. [Reprinted from Botany of the Faeröes. See BOT. GAZETTE **36**:392. 1903.]

Sea currents are regarded as of greatest importance. The pronounced currents from the nearest land do not bathe the islands, but experiments have proved that heavy winds and storms will drive floating objects out of the main currents, and BÖRGESEN believes the general conditions to be favorable to the introduction of algae from the west and north coasts of Ireland, the west coast of Scotland, and the Hebrides, while the currents from east Iceland run straight to the Faeröes. It is also possible that algae may be introduced from the west coast of Norway. Fragments of the algae may drift for many days, especially such as are provided with bladder-like floats, or their spores may be so carried, and floating pieces of timber covered with algal growths are known to travel long distances. Smaller algae of the littoral flora are very likely to be introduced with mud upon the feet and bodies of birds. Finally BÖRGESEN believes that algae may be introduced through the shipping which visits the islands.

These are merely some of the most striking conclusions in an account that is full of interesting observations on the life conditions and habits of marine algae.—B. M. DAVIS.

Plant diseases.

FREEMAN has produced a finely illustrated volume on plant diseases,[2] the first part of which is devoted to a discussion of fungi in general, while the second special part treats of specific fungous diseases of plants. The object of this book, as set forth in the preface, is "rather educational than immediately practical." It is an attempt to give a general account of the nature of fungi, for the purpose of encouraging study on the part of farmers and horticulturists rather than the habit of dependence upon rules and formulae. On this account the scope of the work becomes rather broader than would be indicated by the title, *Minnesota plant diseases*.

The first part comprises a discussion of the morphology, physiology, and ecology of fungi; but, while this part contains much excellent material, the arrangement lacks the logical sequence of first importance in a book of an educational character. It consists rather of a series of interesting pictures without due regard to pedagogical principles. This is likely to leave the mind of the reader confused. The sub-headings of the first chapter on nutrition are as follows: What the fungi are; The fungus method of obtaining nutrition; How the nutritive method is expressed in structure; Parasitism and saprophytism; Storage organs; Fungus shoestrings or strands; Physiology of the mycelium. Then, in chapter III, Fungus life methods, we have as the first subhead, again, Parasitism and saprophytism, the rest of the chapter dealing with habits or rather habitats of different fungi. Too great an effort is made to avoid scientific terms. Thus we have such confusing combinations as "spore-like swimming-spore-cases," "Sac-spore-capsule." It would seem that the reader who can comprehend the allusions to the phylogenetic relationships between fungi and algae would not find it too difficult to comprehend a few scientific terms.

[2] FREEMAN, E. M., Minnesota plant diseases. Imp. 8vo. pp. xxiii+432. *figs.* 211. St. Paul: Report of the Survey. Bot. Ser. V. 1905.

The second part of the book is devoted to descriptions of special diseases. These are classified according to the nature of the crops on which they occur, as follows: Timber and shade trees; Field and forage crops; Garden crops; Orchards and vineyards; Greenhouse and ornamental plants; Wild plants. Under those heads the groups of fungi, as rusts, smuts, mildews, etc., are kept together.—H. HASSELBRING.

Regeneration.

WITH THE TITLE *Studies in regeneration* NĚMEC[3] has published in rather voluminous form the results of his investigations on the regeneration of root-tips. The general conclusions may be briefly summarized as follows. Cutting a transverse section just at the tip results in the regeneration of a new tip in a radial manner. The dermatogen and outer part of the periblem takes no part in this, the new tissue arising from the inner part of the cortex and the plerome. There is first of all the formation of a callus of hypertrophied cells, between which and the meristem arises the group of initials by which the new root-tip is organized. This group is radial from the beginning, the majority of its cells arising from the plerome, only the peripheral ones coming from the periblem. Proceeding back from the tip, the capacity for regeneration diminishes from the periphery inwards, soon disappearing from the periblem. As long as the central cells of the plerome still possess this capacity the regeneration is radial. Farther back it is confined to the pericambium and cells of the periblem and plerome immediately adjoining, which give rise to a ring of meristem, out of which usually more than one root-tip arises. When the capacity of the inner cells of the periblem and the outer cells of the plerome to take part in regeneration is lost, the replacement of the removed root-tip occurs only through the origin of lateral roots, which arise in the pericambium.

When the root is cut through obliquely, the regeneration of the new root-tip occurs at the part of the cut surface nearest the tip. When the tip is slit lengthwise each half re-forms a new tip. If a tip is slit lengthwise for about 1^{mm}, and then one of the halves is removed by a transverse incision, the remaining half regenerates a new half, and also, at the surface formed by the transverse cut, a new tip is developed. Lateral incisions to produce new roots must go at least half way through the plerome. Unless such an incision is made just back of the tip a new tip is soon organized immediately above the cut. The original tip is pushed to one side and finally is displaced entirely. When the incisions are made on two opposite sides of the root at different levels, new root primordia arise at each place, but only the one nearest the original tip continues to develop. If two incisions are made, on opposite sides and at the same level, a new root arises at each, but one is soon suppressed, while the other develops and finally replaces the original tip. About forty-eight hours after the wounding, starch usually appears in the cells of the periblem just above the cut. The grains are not yet

[3] NĚMEC, B., Studien über die Regeneration. Imp. 8vo. pp. 387. *figs. 180.* Berlin: Gebrüder Borntraeger. 1905. *M* 9.50.

mobile, and are aggregated about the nucleus. In about twenty-four hours more, however, they become statoliths and fall to the bottom of the cells. During this time the original tip has been losing its starch, and there is a period of from forty-eight to seventy-two hours in which the old tip has lost its starch and the new tip has none in a movable form. During this period the roots are ageotropic.

In ferns the root-tips do not regenerate. Tips cut off transversely just back of the apical cell are unable to organize a new one, though they may continue growing for several weeks. As the statolithic starch is in the root-cap, and this does not regenerate, such roots remain ageotropic.

Besides the discussion of the experiments, a number of chapters are devoted to a discussion of such topics as the influence of external conditions on regeneration, polarity and regeneration, growth and regeneration, purposefulness of regeneration, relation between geotropism and the presence of statocytes, and other interesting topics connected with regeneration.

As the root-tip regenerates from so many kinds of injuries that could never occur in nature Němec considers that at least in the great majority of cases the capacity could not have arisen because of its utility. The immediate stimulus, he thinks, does not lie among nutritive changes, or arise from the wound, but is a phenomenon of correlation, due to the breaking of the connection between the vegetative tip and the root meristem.—W. B. McCallum.

Plant histology.

Chamberlain has revised and rewritten much of his *Methods in plant histology*,[4] adding several new chapters, elaborating and in many instances shortening the processes. Several new formulae are given for killing and fixing. The paraffin method has been notably improved and the celloidin method has been treated at greater length. A method for embedding in soap is also given.

The new chapters deal with microchemical tests, free-hand sectioning, special methods, the use of the microscope, and micrometric methods involving the use of the camera lucida. A very important new chapter deals with methods of staining filamentous algae and fungi and mounting them in Venetian turpentine. An abstract of the methods of Pfeiffer and Wellheim is given, together with such modifications as have been found to give successful preparations. Delicate forms like Vaucheria can be carried through the stains and finally mounted in Venetian turpentine without showing the least trace of plasmolysis, and even if slight plasmolysis should occur it can be corrected by manipulation of the mounting medium. Preparations made by this method are exceedingly brilliant and show a wealth of detail not possible with other methods. For example, the two nuclei in zygospores of Spirogyra can be readily seen with a low magnification. The Venetian turpentine method, which gives preparations requiring no sealing and as hard and durable as balsam mounts, should almost entirely replace the glycerin method.

[4] Chamberlain, Charles J., Methods in plant histology. pp. x+262. *figs. 88*. Chicago: The University of Chicago Press. 1905. Net $2.25; postpaid, $2.39.

Much attention is given to collecting and keeping material alive in the laboratory. KLEBS's method of securing reproductive phases in algae and fungi is presented in a practical manner. Specific directions are given for making such preparations as are needed by teachers and by those who wish to get a comprehensive view of the plant kingdom from the lowest to the highest forms. The book will be useful to those who wish to keep in touch with modern microtechnique.—W. J. G. LAND.

Bibliographical index of North American fungi.

THE compilation of a bibliographical index of North American fungi by FARLOW[5] is one of the most serviceable tasks ever undertaken in the interests of American systematic mycology, and the publication of it by the Carnegie Institution one of its best contributions to the promotion of botany. The work is the outgrowth of an effort to bring together references to all North American species in the form of a card catalogue. This was begun in 1874, at a time when there was no complete record of the species known from North America. Within a few years of its inception Mr. A. B. SEYMOUR was entrusted with the details of this herculean labor, under Dr. Farlow's direction, and his painstaking fidelity is worthy of recognition.

It is the aim of the work to include all references having any bearing on the taxonomy of fungi occurring in countries north of the Isthmus of Panama, the scope of the original plan (which was restricted to the region north of Mexico) having been greatly extended, on account of the close connection of species from our southern border with those of Mexico, Central America, and the East Indies. References to works of purely morphological, cytological, and physiological interest have been excluded; so have purely popular accounts, unless they were of use in giving distribution of the species or in furnishing good illustrations. In nomenclature the work is conservative. The principle of adopting the oldest specific name has been generally followed. Where the vagueness of older descriptions has made it uncertain to what species they applied the writers have had no scruples in rejecting the older names.

The index itself is arranged alphabetically. The names are printed in boldface type, synonyms and cross references being in italics. The citations, arranged in chronological order under each name, follow the form adopted by the Madison Botanical Congress in 1893 and by Section G, A.A.A.S. in 1894. In many cases of confused synonomy, critical examinations were made of authentic specimens and the related literature. Notes of interest obtained thus are added under the species in question. The present part, which is part I of the first volume, includes names from *Abrothallus* to *Badhamia*.—H. HASSELBRING.

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[5] FARLOW, W. G., Bibliographical index of North American fungi. Vol. I, part 1. 8vo. pp. xxxv+312. Washington: Carnegie Institution. 1905.

MINOR NOTICES.

Japanese vegetation.—Professor MIYOSHI, of the University of Tokyo, has begun the publication of photogravures of Japanese vegetation,[6] to represent wild and cultivated plants and plant societies. Each picture is on a separate sheet of cardboard 20.5×27^{cm}, the size of the print being 16×23^{cm}. Accompanying the illustrations is a descriptive text in both English and Japanese. The author has not yet determined the number of plates to be issued. So far, two parts have appeared, part I containing eight plates of cultivated and semi-cultivated plants, and part II containing eight illustrations of the vegetation of the island of Nikko.

The illustrations are well chosen and well made. Among the most effective and characteristic are the long avenues of giant mountain cherry trees, gorgeous with their spring blossoms, the graceful bamboos bending beneath their burden of winter snow, and the forest vegetation around the Hannya waterfall. The descriptive text is precise, and interspersed by interesting remarks which show that the author has an eye for color and setting.

It is to be hoped that the series may be continued to give us many more illustrations of the flora of this interesting country.—F. C. NEWCOMBE.

A botanical cyclopedia.—An illustrated German dictionary of botanical terms has appeared under the editorship of CAMILLO K. SCHNEIDER,[7] with the assistance of a number of other German botanists. This volume of almost 700 pages presents much more than a list of definitions, for there are illustrated descriptions of the morphology and minute structures of organs, of the sort one would expect to find in a cyclopedia. The terms, of course, are those employed in the German language, and the work will not take the place, for the English or American botanist, of JACKSON'S excellent *Glossary of botanic terms*. —B. M. DAVIS.

NOTES FOR STUDENTS.

Chemotaxis of spermatozoids.—The chemotaxis of the spermatozoids of Isoetes has been studied by SHIBATA.[8] In *Isoetes japonica*, which was used for the study, the sporangia ripen in autumn. Microspores, sown in tap water in Perti dishes late in November, begin to germinate about the middle of January. The duration of the swarming movements of the spermatozoids is shorter than in the ferns, vigorous movements lasting only about five minutes; some movement of

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[6] MIYOSHI, M., Atlas of Japanese vegetation. With explanatory text. Tokyo: Maruzen Kabushiki Kaisha. 1905.

[7] SCHNEIDER, C. K., Illustriertes Handwörterbuch der Botanik. Imp. 8vo. pp. 690. *figs. 341*. Leipzig: Wilhelm Engelmann. 1905. *M* 16.

[8] SHIBATA, K., Studien über die Chemotaxis der Isoetes-Spermatozoiden. Jahrb. Wiss. Bot. **41**:561–610. 1905.

the spermatozoid, however, may continue for ten or fifteen minutes, and of the cilia for five minutes longer. PFEFFER'S capillary method was used in the experiments. The principal headings are: position chemotaxis, relation between the intensity of the stimulus and extent of the reaction, repulsion by free acids and alkalis, negative chemotaxis with the ions of heavy metals, repulsive effect of alkali salts, behavior with osmotically acting substances, repulsive effect of ions of certain organic acids, the action of narcotics, theoretical, and review.

Malic acid acts as a strong topochemotactic stimulus and may be regarded as the specific stimulant for the spermatozoids of Isoetes, although certain other substances also exert some topochemotactic influence. Free malic acid in weak solutions exerts a positive chemotactic influence, but in stronger solutions a negative one. The salts of various metals act as negatively chemotactic stimuli, as do also the anions of di- and tribasic organic acids, including malic acid. The positive chemotaxis with malic acid is of a typically topotactic nature. The reaction consists in a turning of the body axis of the spermatozoid and a movement toward the source of stimulation. Whether the structure for the perception of chemotactic stimuli consists of the whole body of the spermatozoid or only of localized portions of it is not yet determined.—C. J. CHAMBERLAIN.

Tuberization.—The causes of tuberization still furnish a field for study. BERNARD first supposed that *Fusarium Solani* was the endophytic fungus of the potato; this has since been disproved by GALLAUD and by BERNARD himself, but the identity of the fungus is still undetermined. H. JUMELLE[9] has been conducting experiments on *Solanum Commersoni*, a tuber-bearing species related to the potato, but as yet his results are largely negative. The chief interest attached to his studies are occasioned by the fact that *S. Commersoni* has small slowly developing tubers placed on long stolons; these are the very characters which the potato is said to have had when first introduced into Europe, before the endophytic fungus became sufficiently abundant. *S. Commersoni* was infected by fungi from *S. tuberosum*, but, as stated above, with negative results. JUMELLE thinks that with suitable infection, it may be possible to secure tubers like those of the potato, and further experiments are in progress. It should be said that GALLAUD thinks that BERNARD has not yet isolated the true tuber-forming fungus.—H. C. COWLES.

Two parasitic fungi.—KLEBAHN[10] has worked out the life histories of two common species of the so-called Imperfecti group. The first of these is the common elm fungus, *Phleospora Ulmi* (Fr.) Wallr. This is connected with an ascomycetous form, which appears on the infected dead leaves during the winter and ripens in spring, when the spores are ejected and infect the young

[9] JUMELLE, H., Del'influence des endophytes sur la tubérisation des Solanum. Rev. Gén. Bot. **17**:49–59. 1905.

[10] KLEBAHN, H., Untersuchungen über einige *Fungi imperfecti* unddie zugehörigen Ascomycetenformen. I. u. II. Jahrb. Wiss. Bot. **41**:485–560. *figs.* 75. 1905.

elm leaves. The form is named *Mycosphaerella Ulmi* Klebahn[11]. Both conidia and ascospores produced identical mycelia in cultures. The Phleospora was produced by sowing ascospores on the under side of elm leaves. No infection took place from spores sown on the upper surface. The study of *Gloeosporium nervisequum* (Fckl.) Sacc. revealed a rather complicated series of forms belonging to this fungus. An ascogenous stage develops on the dead leaves, as in Phleospora. This is *Gnomonia Veneta* Klebahn. Beside the usual conidial form and the ascogenous form, the fungus assumes the form of a Myxosporium on the young branches, and there produces the twig wilt always noticed on sycamore trees affected with the Gloeosporium. A fourth form develops on the dead leaves. This is a conidial form of the Fusicoccum type. Proof of the connection of all these forms rests mainly in the similarity of the mycelia produced in pure cultures from the various spore forms. Infections could not be produced readily, but a few cases of inoculation with ascospores were successful. The various spore forms have been described under different names, which are given in the synonymy.—H. HASSELBRING.

Shore formations in Denmark.—WARMING, in collaboration with WESENBERG-LUND and others in an interesting paper, has correlated the work of plants and animals in the shore formations of western Denmark.[12] A "vad" is a shallow coastal lagoon, cut off from the sea proper by a line of islands, and bare at low tide; the bottom may be of sand or clay, the latter type prevailing in the more tranquil places. The sandworm, *Arenicola marina*, is the most characteristic animal of the sandy "vader" or shallows, and the excrements of this worm are found there in great abundance. Hence it has commonly been thought that these animals have a soil function, similar to that of the earthworm, and that they help to build up the shallow into a marsh. The authors, however, find that Arenicola is very sedentary in its habits, swallows only from surface layers, and that it retards rather than furthers soil enrichment. The waves wash any fine particles landward, leaving the Arenicola shallow as sandy as before and hence well adapted for the continued prosperity of Arenicola. In shallower water closer to the shore, where the bottom material is finer, the amphipod, *Corophium grossipes*, dominates; here the bottom is characteristically red-brown in color and presents a riddled surface appearance. The Corophium shallows teem with animal life, and here the influence of the animals is such as to convert the area somewhat rapidly into a marsh. To this work blue green algae contribute something, but animals are much more important land builders than plants in the Corophium shallows. Large areas of land have been gained from the sea in this way in Denmark, and one case is cited where a fertile meadow has been developed from a barren sandy shallow within two hundred years. In the argillaceous

[11] Preliminary note in Zeitschr. Pfl. krankh. **12**:257. 1902.

[12] WARMING, E., Bidrag til Vadernes, Sandenes, og Marskens Naturhistorie. In collaboration with WESENBERG-LUND, ÖSTRUP, et al., with French résumé. Kongl. Dansk. Vid. Selsk. Skrift. VII. **2**:1–56. 1904.

shallows, in contrast to the above, plants are the more efficient land-builders; the developmental processes in such places are well known and need not be recounted here. WARMING also speaks of sandy plains that are subject to occasional inundation. Here algae play a great part in soil-making; it is common for a layer of Phycochromaceae to penetrate for three to five centimeters into the sand, cementing the grains together, and giving a greenish appearance to the ground. Many of the diatoms characteristic of such places are listed by habitats. The peculiar depressions of salt marshes, called "pans" by OLIVER and TANSLEY, are thought by WARMING to be formed where heaps of decaying vegetation have lain; the consequent destruction of the vegetation makes it easy for the waters to wash out the soil in such places.—H. C. COWLES.

Periodicity of sexual organs in Dictyota.—WILLIAMS, in the third contribution to his series of *Studies in the Dictyotaceae*,[13] discusses the remarkable periodicity in the formation of the sexual cells in Dictyota. The sexual organs are produced during the fruiting season in fortnightly crops, synchronous with the spring tides, and a general liberation of the gametes takes place on a particular day, at a fixed interval after the highest spring tide, varying, however, in different localities. Of the factors (temperature, pressure, aeration, etc.) which fluctuate with the alternation of neap and spring tides, the one which seems to account most satisfactorily for the facts of periodicity is the increased illumination of the plant during the low water of spring tides. The times of initiation and liberation may be slightly accelerated or retarded by exceptional meteorological conditions, as when wind causes a difference of two or three feet in the height of water, or a rise of one inch in the barometer accompanies a depression of six or seven inches in the tide.—B. M. DAVIS.

Brown pigment of algae.—The generally accepted view that the color of the chromatophores of the brown algae and diatoms results from the presence of a brown pigment, phycophaein, in addition to chlorophyll, is challenged by MOLISCH,[14] who believes that the phycophaein extracted from these algae is a post mortem product. He holds that the brown pigment is a single substance, phaeophyll, which passes readily over to chlorophyll when treated with hot water, alcohol, and other fluids. A similar brown pigment is found in the orchid, *Neottia nidus-avis*. Beside the phaeophyll, the brown algae and diatoms contain carotin and a bluish-green pigment, leucocyan.—B. M. DAVIS.

Bracts of Bennettites.—LIGNIER[15] from a reexamination of his preparations of the involucral bracts of *Bennettites Morierei* concludes that in all the sterile scales, superficial or otherwise, which enter into the composition of the strobilus, the terminal enlargement is due to hypertrophy and does not result from a reduction of the bract.—W. J. G. LAND.

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[13] WILLIAMS, K. L., Studies in the Dictyotaceae. III. The periodicity of the sexual cells in *Dictyota dichotoma*. Ann. Botany **19**:531–560. *figs. 6.* 1905.

[14] MOLISCH, H., Ueber der braunen Farbstoff der Phaeophyceen und Diatomeen. Bot. Zeit. **63**[1]:131–162. *pl. 6.* 1905.

[15] LIGNIER, O., Notes complémentaires sur la structure du *Bennettites Morierei*. Bull. Soc. Linn. Normandie V. **8**:(pp. 7.) 1904.

NEWS.

PROFESSOR EDUARD STRASBURGER traveled in Egypt during part of December and January.

DR. OSKAR BREFELD, professor of botany at Breslau, has retired owing to failing eyesight.

MR. WALTER FISCHER has resigned his position as Assistant in Botany at the Ohio State University, and has taken up work in the United States Department of Agriculture, Bureau of Plant Industry.

DR. A. F. BLAKESLEE, who is spending the winter in investigations at Halle, was awarded the Bowdoin prize of Harvard University ($200) last spring for his work on sexual reproduction in black molds.

IN November and December Dr. JOHN W. HARSHBERGER, of the University of Pennsylvania, delivered a series of five lectures on "Weird and marvelous plants" in the Ludwick Institute courses of free lectures, Philadelphia.

DR. ERNEST A. BESSEY has been transferred from Washington to the Subtropical Laboratory of the U. S. Department of Agriculture at Miami, Florida, where he may be addressed in future. Professor P. H. ROLFS, formerly of the Sub-tropical Laboratory has accepted the directorship of the Agricultural Experiment Station of Florida.

A RECENT circular gives an account of the Royal Hungarian Central Institute of Viticulture, the buildings of which were completed in 1904. This institute was initiated in 1896 by a law decreeing the establishment near Budapest of an institution for studying the problems of viticulture and wine-making, and giving scientific and practical instruction in these subjects. In 1898 Dr. ISTVÁNFFI, then professor at the University of Kolozsvar, but perhaps better known from his association with BREFELD during part of the latter's extensive investigations, was called to organize and direct the new institution, whose first work was done in quarters rented until the completion of the new ones. The present buildings are five, each of three stories. The main hall, 66×21^m contains the library, museum, offices, and lecture room. The four smaller halls, all similar in construction, are devoted respectively to the four sections: (1) physiology and pathology, (2) chemistry, (3) zymology, and (4) practical viticulture and oenology. The institution is excellently equipped for carrying on these different branches of work. Its primary object is that of an experiment station whose field is restricted to the wine-growing interests alone; secondarily, provision is made for instruction to advanced students in the practical aspects of viticulture and oenology.